

The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Capitata Part 1

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The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Capitata Part 1. - This study reviews all European hydrozoan species belonging to the capitata families Acaulidae, Boreohydridae, Candelabridae, Cladocorynidae, Cladonematidae, Margelopsidae, Pennariidae, Protohydridae, and Tricyclusidae. Updated diagnoses for the families and genera are provided and existing taxonomic problems solved or at least outlined. *Candelabrum verrucosum* Bonnevie, 1898 is regarded as a valid species and redescribed based on a new record from Greenland. Although *Spadix purpurea* Gosse, 1853 may be a senior synonym of *Candelabrum cocksii* (Cocks, 1854), the latter is regarded as the valid name, this because the former name has not been used after 1899, while the latter has been widely used [ICZN article 23.9.1.1]. Likewise, two senior synonyms of *Eleutheria claparedii* Hartlaub, 1898 are declared as invalid as they have never been used since their original introduction by Haeckel.

Keywords: Marine invertebrates - Cnidaria - Hydrozoa - Anthoathecata - Capitata - descriptions - revision - taxonomy.

INTRODUCTION

This publication is the second in a series of taxonomic revisions of the European Anthoathecata (=Anthomedusae, Athecata) which was begun with the families Oceanidae and Pachycordylidae (Schuchert, 2004). Although it was initially planned to continue with families of the suborder Filifera, some essential material could not be obtained to complete them in time. Therefore, this second paper presents some families of the suborder Capitata.

Following the suggestions of fellow colleagues, the geographic scope of the fauna under investigation has been somewhat extended to match the territory covered by the European Register of Marine Species (Costello *et al.*, 2001). The new scope now also includes the Azores, Iceland, eastern Greenland, Jan Mayen, the Barents Sea, Svalbard, and Franz Joseph Land. The extension of the geographic scope does not add many species. A single species needs to be added to the families treated in the first paper of this series, namely *Similomerona nematophora* (Antsulevich, 1986). This species is already mentioned and diagnosed in Schuchert (2004), but its type locality was erroneously given as "Kurile Islands". Dr Antsulevich informed me that the

species was described from material originating from the archipelago of Franz Joseph Land, thus falling within the limits of the newly adopted coverage. Furthermore, although the paper was authored by Antsulevich & Polteva (1986), the authorship of the species name is due to Dr Antsulevich alone. Although the genus name *Merona* is an artificial word, its ending is characteristic for the feminine gender, thus requiring a change of the specific epithet to *nematophora*.

The current paper treats several families of the suborder Capitata. The families reviewed here were chosen somewhat arbitrarily and do not form a natural unit, though some are evidently closely related. The selection had to be based on the material available for study. The order of the families as given below has no phylogenetic significance and is only thought to group somewhat similar forms together. For a phylogenetic analysis of these families see Petersen (1990). Molecular phylogenies of some families of Capitata can be found in Collins *et al.* (2005a, and b).

MATERIAL AND METHODS

For morphological methods see Schuchert (1996; 2004) or Bouillon *et al.* (2004). Where possible, it was attempted to supplement the species descriptions by 16S DNA sequence information. The methods to obtain 16S DNA sequences are described in Schuchert (2005). All sequences have been submitted to the EMBL database under the accession numbers: AM088481, AM088482, AM088483, AM088484, AM088485. The origin and identity of the material used to obtain 16S sequence data are given for each species in the section "Material examined". Some sequences have been determined by other laboratories using material described here (accession numbers AY920796, 18S AY920758, AY787879, AY920762, AY512539). Morphological characters of the Cladonematidae were used for a phylogenetic analysis using the parsimony criterion and the program PAUP* (Swofford, 2001). Bootstrap replicates were performed 1000 times. Only a subset of all Cladonematidae was used. The members of the genus *Cladonema* are all very similar and well represented by *C. radiatum*. For *Staurocladia*, only those species with known life cycle were used. As out-group taxa, three members of the Corynidae were used (comp. Schuchert, 2001b). Table 1 gives the species names and the characters used and their states.

ABBREVIATIONS

BMNH	The Natural History Museum, London, England
MHNG	Muséum d'histoire naturelle de Genève, Switzerland
ICZN	International Code of Zoological Nomenclature
IRSN	Institut Royal des Sciences Naturelles de Belgique, Bruxelles
ZMUC	Zoological Museum Copenhagen, Denmark
CI	Consistency index
RI	Retention Index
HI	Homoplasy Index

TAXONOMIC PART

FAMILY ACAULIDAE FRASER, 1924

DIAGNOSIS: Solitary hydroids, body divided into basal and distal part. Basal part conical to cylindrical, covered or not by gelatinous perisarc which may form anchoring

filaments. Upper part with few indistinctly capitate tentacles or many capitate tentacles, lowest whorl of capitate tentacles may transform into thick filiform tentacles. Gonophores fixed sporosacs in the lower or middle part of the hydranth. Sometimes asexual reproduction by transverse fission.

REMARKS: The name Acaulidae was proposed by Fraser (1924) and this spelling was used by all subsequent authors. According to the ICZN [article 29.3.1.1] there is thus no need to change it to the formally correct Acaulididae.

According to Bouillon (1985), this family contains two genera: *Acaulis* Stimpson, 1854 and *Acauloides* Bouillon, 1965. Petersen (1990) also included the genus *Boreohydra* Westblad, 1937 in the Acaulidae, while Bouillon (1985) kept *Boreohydra* in a separate family Boreohydridae, this together with the genus *Protohydra*. A third genus was later added to the Acaulidae by Thomas *et al.* (1995): *Cryptohydra*. The discovery of *Cryptohydra* narrowed the gap of the Acaulidae to the genus *Protohydra* – and thus Boreohydridae – to a degree that any subdivision now appears entirely arbitrary. The proximity of both families is further emphasized if the nematocyst warts on the body of *Boreohydra* are regarded as reduced capitate tentacles (Calder, 1974). It is thus tempting to fuse both families, but this should only happen in the framework of a broader analysis and discussion and the phylogenetic relationships. The Acaulidae and Boreohydridae have also many similarities with the Candelabridae and Tricyclusidae, and the demarcations are equally arbitrary. Because a phylogenetic analysis based on morphological characters alone appears not so promising (see Petersen, 1990), it is therefore preferable to wait with a revision until a thorough molecular analysis provides the necessary robust phylogeny. Meanwhile, the classification according to Bouillon (1985) is here used in order to maintain nomenclatural stability.

Through monotypy, the genus *Acauloides* Bouillon, 1965 is unfortunately based on *Acauloides ammisatum*, an insufficiently known species. *Acauloides* is thus essentially distinguished from *Acaulis* through the absence of filiform tentacles. The filiform tentacles of *Acaulis* are formed relatively late in development through the transformation of capitate tentacles (Berrill, 1952). Using this ontogenetic argument and also outgroup comparisons to the Tricyclusidae and Candelabridae, it is evident that filiform tentacles of *Acaulis* are apomorphic. The absence of filiform tentacles in the genus *Acauloides* is thus a plesiomorphic trait and unsuitable to reveal a monophyletic group. The genus *Acauloides* could nevertheless be valid, as in *Acauloides ilonae* the gonophores develop in the upper axils of the tentacles, which is clearly an apomorphy for this genus. Because *Acauloides ilonae* is perhaps a synonym of *A. ammisatum*, it is thus recommendable to continue to use the genus *Acauloides* in order to maintain nomenclatural stability.

KEY TO GENERA:

- 1a hydranth small, very elongated, all tentacles indistinctly capitate
 *Cryptohydra* (not in European fauna)
 1b majority of tentacles distinctly capitate 2
 2a mature hydranth with a whorl of thick filiform tentacles *Acaulis*
 2b all tentacles capitate *Acauloides*

Genus *Acaulis* Stimpson, 1854

TYPE SPECIES: *Acaulis primarius* Stimpson, 1854.

SYNONYMS: *Blastothela* Verrill, 1878: 374; ? *Myriocnida* Stechow, 1909 (invalid *nomen nudum*).

DIAGNOSIS: Hydroid connected to substrate by modified hydrocaulus secreting a gelatinous sheath or forming anchoring filaments; hydranth fusiform; capitate tentacles in one oral whorl and more scattered below, solid, with chordoid gastrodermis; below capitate tentacles one whorl of filiform, long, stout, aboral tentacles developing by transformation of capitate tentacles; gonophores fixed, carried singly or in clusters on short pedicels.

REMARKS: Stechow (1909) introduced the genus name *Myriocnida* for a hydroid described in Fewkes (1890) as *Acaulis* (without specific epithet). Because it was not based on a nominal species, the genus is not valid. It remains unclear to which species Fewkes' material belonged (he described it from notes made by someone else). It could have been either *Acaulis* or more likely an incomplete *Candelabrum* species.

Acaulis primarius Stimpson, 1854

Fig. 1

Acaulis primarius Stimpson, 1854: 10, pl. 1 fig. 4; Allman, 1872: 378; Sars, 1874: 123, pl. 5 figs 14-20; Will, 1913: 57, pl. 26; Scheuring, 1922: 167, pl. 5 fig. 1; Berrill, 1952: 17, fig. 6; Rees, 1957: 466, fig. 13; Bouillon, 1971: 342, pl. 4; ? Verwoort, 1985: 269, plate 1; Schuchert, 2001a: 35, fig. 22A-D.

Acaulis primaris – Naumov, 1969: 243, fig. 112 [incorrect subsequent spelling].

MATERIAL EXAMINED: Material from Iceland and Greenland as given in Schuchert (2001a).

DIAGNOSIS: Acaulidae with filiform tentacles in mature animals, sporosacs not in axils of tentacles, base without attachment filaments.

DESCRIPTION: Solitary hydroids, body thickly fusiform to cylindrical, divided into basal part (approx. 1/5 of height, variable) and upper part. Both parts separated by one whorl of five to eight thick tapering tentacles covered evenly with nematocysts. Basal part conical to cylindrical, surrounded by thick jelly covered by adhering detritus. Upper part of hydranth roughly cylindrical with up to 50 scattered capitate tentacles; hypostome rounded. Gonophores on lower part of region with capitate tentacles but not associated with the tentacles. Gonophores sessile sporosacs with spadix but without radial or ring canals. Nematocysts: stenoteles, microbasic heteronemes (euryteles or mastigophores), and desmonemes.

DIMENSIONS: Mature polyps are 5 to 10 mm in height, extended up to 2 cm (Westblad, 1947), gonophores ca. 0.5-0.6 mm. Nematocysts: stenoteles, (18-21)x(14-17) mm; heteronemes, (16-20)x(7-10.5) mm; desmonemes, (12-15.5)x(8.5-10.5) mm.

DEVELOPMENT: Young hydranths have no filiform tentacles, only capitate ones. During growth, the lowest capitate tentacles become elongated and thicker, and the nematocyte free regions of the tentacles are subsequently covered by nematocytes (see Fig. 1A-B) (Berrill, 1952). The development of the gonophores can begin before the filiform tentacles have completed their transformation.

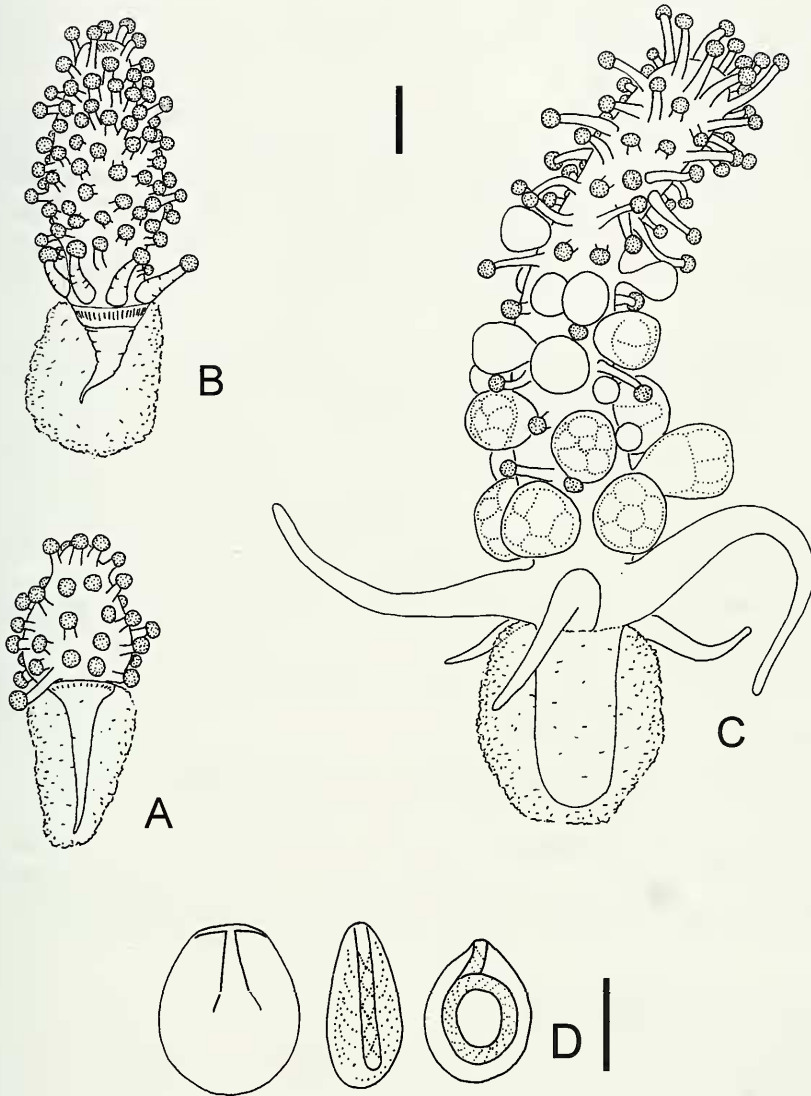


FIG. 1

Acaulis primarius Stimpson, 1854; after Schuchert (2001a), Icelandic material. A) Juvenile, scale bar 0.5 mm, also valid for sections B-C. B) Intermediate sized specimen with beginning transformation of lowest tentacles. C) Mature female, filiform tentacles fully developed. D) Nematocysts, as seen in preserved material: stenotele, microbasic heteroneme, desmoneme, scale bar 10 μ m.

ADDITIONAL DATA: Westblad (1947) describes and depicts both the gonophore development and gametogenesis. Westblad (1947) also depicts the nematocysts and describes their distribution.

BIOLOGY: *Acaulis primarius* lives usually partially embedded in sediment bottoms at depths of down to 350 m, usually not above 20 m depth (Berrill, 1952; Schuchert, 2001a).

DISTRIBUTION: Northern Atlantic, Arctic to boreal regions; New England, New Brunswick, north-west coast of Norway, Barents Sea, White Sea (Scheuring, 1922; Fraser, 1944; Naumov, 1969), North Sea, Sweden (Jäderholm, 1909; Westblad, 1937; Bouillon *et al.*, 1995), Baltic Sea (Will, 1913; Schönborn *et al.*, 1993), Iceland (Schuchert, 2001a), western Greenland (Schuchert, 2001a). Perhaps also Bay of Biscay (Vervoort, 1985, identification uncertain). Type locality: Grand Manan, Bay of Fundy, Canada.

REMARKS: Stimpson (1854) described *Acaulis primarius* based on two sets of animals collected at different times. The first animal he found and depicted corresponds exactly to our current concept of *Acaulis primarius*. The second set he found later, attached to red-algae (it is unclear in what depth, he states 5-15 f., which could be feet or fathoms, both interpretations can be found in the literature, but the latter being more probable). In the second set of specimens the tentacles were much longer, the hydranths resembled a corynid and they reportedly produced medusae. Allman (1872), Will (1913), and Fraser (1924) noticed this difference and assumed that the second set of Stimpson's material belonged to another species than *Acaulis primarius*. Allman (1872) restricted the scope of *Acaulis* to the animal depicted in Stimpson (1854), thus he *de facto* selected a lectotype and *Acaulis primarius* is thus well defined.

Genus *Acauloides* Bouillon, 1965

TYPE SPECIES: *Acauloides ammisatum* Bouillon, 1965, by monotypy.

SYNONYMS: ? *Psammocoryne* Monniot, 1962 (invalid *nomen nudum*).

DIAGNOSIS: Hydroid attached to substrate by modified hydrocaulus, secreting a gelatinous sheath or mucous film; capitate tentacles in one oral whorl and more scattered below, solid, with chordoid gastrodermis; without filiform tentacles; gonophores in upper axils of tentacles, asexual reproduction through transverse fission.

Acauloides ammisatum Bouillon, 1965

Fig. 2

? *Psammocoryne*. – Monniot, 1962: 274, fig. 14b [*nomen nudum*].

Acauloides ammisatum Bouillon, 1965: 54; Bouillon, 1971: 335, figs IV8-11, V-VI; Bouillon *et al.*, 2004: 86, fig. 47H.

MATERIAL EXAMINED: None, type material could not be located.

DIAGNOSIS: Acaulidae with capitate tentacles only, adults 0.6-2 mm, 10-25 tentacles, peduncle without gelatinous tube, only mucous secretion at its end for attachment to sand grains.

DESCRIPTION: Solitary hydroids, thick fusiform shape, short peduncle of about 1/3 of total height, peduncle without gelatinous tube but at end mucous secretion by which the animal attaches itself to sand grains. Tentacles all capitate, 10-25, one oral whorl of 4-6 short tentacles, remaining scattered below on body, those in middle of body longest, others very short to almost lacking a stalk. Nematocysts: stenoteles;

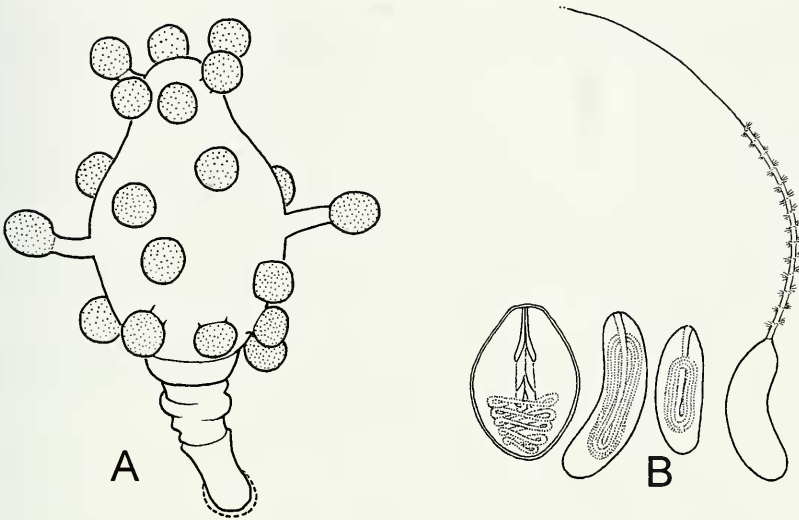


FIG. 2

Acaulooides ammisatum Bouillon, 1965; modified after Bouillon (1971), no scale given. A) Polyp. B) Stenotele, larger mastigophore, smaller mastigophore, discharged mastigophore.

desmonemes; holotrichous microbasic mastigophores, when discharged shaft longer than capsule. Vegetative and sexual reproduction not known.

DIMENSIONS: Polyps 0.6-2 mm. Nematocysts: stenoteles $17 \times 14 \mu\text{m}$, desmonemes $6 \times 10 \mu\text{m}$, microbasic mastigophores $(16-18) \times (6-8) \mu\text{m}$.

ADDITIONAL DATA: Bouillon (1971) provides further details on the histology and cytology of this species.

DISTRIBUTION: Roscoff, Brittany; ? Banyuls-sur-Mer (Mediterranean). Type locality: Roscoff, English Channel.

REMARKS: *Acaulooides ammisatum* Bouillon, 1965 strongly resembles the vegetative reproduction stage of *A. ilonae* (Brinckmann-Voss, 1966) and the two are possibly conspecific. There are some minor size differences, with *A. ammisatum* being smaller and having slightly larger nematocysts. Another formal difference is the absence of a gelatinous tube in *A. ammisatum*, for which only a mucous cover has been described. However, such a mucus cover might be only the initial stage of a gelatinous tube, a type of cover which is only seen in fully grown animals. There is also a possible ecological difference: while *A. ammisatum* occurs on sand, *A. ilonae* has been found on mud only. More data – especially on mature animals from Roscoff – are needed before a final more definite conclusion is possible. Meanwhile, both nominal species should be kept separate.

Bouillon (1971) also attributed to this species some animals from Banyuls (Mediterranean) depicted in Monniot (1962). Monniot found her animal in coarse sand and identified it as *Psammocoryne*. This name is not a valid genus as it was not asso-

ciated with a valid nominal species. Furthermore, Monniot's hydroid could easily also be referred to *A. ilonae* and it is therefore also somewhat unclear whether *A. ammisatum* also occurs in the Mediterranean (this in case that they are not conspecific).

Acauloides ilonae (Brinckmann-Voss, 1966)

Fig. 3

Acaulis ilonae Brinckmann-Voss, 1966: 292, figs 1-10; Brinckmann-Voss, 1970: 44, text-fig. 51, pl. 1 figs 4-6.

Acauloides ilonae – Bouillon *et al.*, 2004: 86, fig. 47I.

MATERIAL EXAMINED: Syntypes (labelled holotype), BMNH 1963.12.9.1, as *Acaulis ilonae*, two specimens, both broken. – BMNH 1974.11.21, as *Acaulis ilonae*, Naples, 20.10.1960-29.11.1961, leg. Brinckmann-Voss, one female, pedicel broken off.

DIAGNOSIS: Acaulidae with capitate tentacles only, sexually reproducing adults 5-10 mm, about 2 mm in phase of vegetative reproduction; sporosacs in upper axils of tentacles, peduncle of adult hydranths in gelatinous sheath.

DESCRIPTION (after Brinckmann-Voss, 1966; 1970; and own observations): Mature hydroid spindle shaped, divided into two parts of roughly the same length: an upper tentacle-bearing part and a basal part without tentacles called peduncle (or "foot"). Peduncle tapering, surrounded by a gelatinous sheath which adheres to mud particles or cultivation vessels, gastrodermis highly vacuolated. Tentacles all capitate, solid, up to 60, one oral whorl of four to five tentacles and a basal whorl comprising the same number of tentacles, between them a number of scattered tentacles, often in groups of two to three around a sporosac, tentacle length unequal, longest ones more proximal, diameter of capitula also variable. Gonophores are sporosacs without radial canals, developing always in upper axils of tentacles in middle region of tentaculate part, oldest sporosacs in middle, younger ones proximal and distal to them. New tentacles often formed close to the gonophores. Colour of the animals pink to orange, with a number of white dots on surface, very old specimens have a brownish colour, nematocysts: stenoteles, microbasic euryteles and desmonemes. Fertilized eggs developing a capsule and going through an encysted resting stage.

Polyps in vegetative phase of reproduction small, with 29-35 tentacles, attached to substratum, multiplying by binary fission in region of tentacles.

DIMENSIONS: Sexually reproducing animals up to 10 mm, polyps in phase of vegetative multiplication up to 2 mm. Diameter of eggs 0.15 mm. Nematocysts: desmonemes (8.4-12.6) × (7.6-9.2) μm; stenoteles (18.5-22.7) × (16.0-19.3) μm; microbasic euryteles (11.8-14.3) × (3.4-7.6) μm (Brinckmann-Voss, 1966).

DISTRIBUTION: Naples, questionably also Roscoff, Brittany, although the latter records may refer to *A. ammisatum*. Type locality: Gulf of Pozzuoli, Naples, Italy, 45 m.

BIOLOGY (after Brinckmann-Voss, 1966; 1970): *Acauloides ilonae* is able to creep sluggishly on the substrate. The animals are gonochoristic; female and male hydroids continue to spawn their gametes several times for more than a year, the gametes differentiate continuously. Eggs are usually shed during the night and early morning hours, fertilisation takes place in the seawater. The embryo does not swim and attaches itself to the ground and transforms into a flattened body which is covered with thin, transparent cuticula. The cyst remains attached for at least one month, after which a

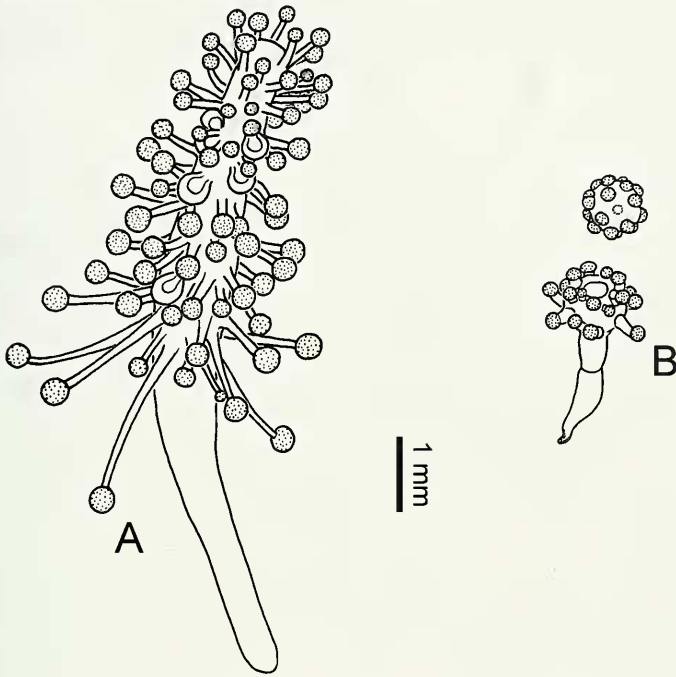


FIG. 3

Acauloides ilonae (Brinckmann-Voss, 1966), modified after Brinckmann-Voss (1966), scale bar 1 mm. A) Sexually reproducing polyp. B) Vegetatively reproducing polyp just after fission, with aboral and oral parts.

small polyp without tentacles hatches very slowly (it takes 2-3 days). Hydroids hatch from cysts only if kept in water of 13°C, at 20°C the hatching rate is poor. The young polyp grows to a size of about 2 mm and then starts the vegetative reproduction phase by transverse fission. At 20°C divisions take place every 10-45 days and if kept at 20° the fission continues, the polyps do not exceed 2-3 mm, and they do not develop gonophores. Polyps that had undergone divisions and are brought to 13° do not divide anymore, they begin to grow in length, get more tentacles and develop gonophores in the axils of the tentacles, thus starting the sexual phase. Individuals that had hatched from cysts and are cultured at 13° undergo one or two rounds of divisions before they develop gonophores. Sexual maturity is not reached without having first undergone asexual division.

The hydroid was found on surface of mud in depths of 20 to 80 m. It occurred in abundance around Naples from November to April. It was not found from July to October. It is thus a winter species.

REMARKS: Brinckmann-Voss (1966) described her material based on animals from Naples, but also mentioned that Bertil Swedmark had found it at Roscoff too (via personal communication by J. Rees). Because it appears that the latter material was

more likely *Acaulooides ammisatum* (see remarks in Bouillon, 1971: 335), the occurrence of *A. ilonae* outside the Mediterranean is uncertain (if the two indeed prove to be distinct species, see remarks under *A. ammisatum*).

FAMILY BOREOHYDRIDAE WESTBLAD, 1947

TYPE GENUS: *Boreohydra* Westblad, 1937.

DIAGNOSIS: Hydroids solitary, small, with one whorl of reduced tentacles, capitate or not, located in the oral or median part of body; perisarc covering of base filmy or absent; gametes in body wall.

REMARKS: Representing likely a simplified form, the affinities of the genus *Boreohydra* with its sole species *B. simplex* remains controversial. Westblad (1947) considered it related to the Tubulariidae, but sufficiently distinct to deserve being placed in a separate family. Rees (1957) could not agree and placed it in the Corymorphidae. Calder (1974) thought that if the nematocyst clusters on the body should prove to be nothing but reduced capitate tentacles, then the genus should belong to the Candelabridae. Bouillon (1985) considered the family Boreohydridae as valid and added also the genus *Psammohydra* to it, this because of the resemblance of their cnidome. Petersen (1990) placed *Boreohydra* among the Acaulidae, but gives no arguments for this and he does not discuss *Psammohydra*. As already stated for the family Acaulidae, the problem is not resolvable by traditional approaches and, pending a molecular analysis, the family *Boreohydridae* is here retained for the time being.

KEY TO THE GENERA:

- 1a hydranth with oral capitate tentacles and nematocyst buttons on body *Boreohydra*
 1b filiform tentacles in middle of body; hypostome proboscis-like *Psammohydra*

Genus *Boreohydra* Westblad, 1937

TYPE SPECIES: *Boreohydra simplex* Westblad, 1937.

DIAGNOSIS: Solitary hydroids of small size, living buried in the sediment; caulus covered by filmy perisarc; one whorl of capitate tentacles near mouth and numerous scattered nematocyst clusters on hydranth body. Gametes in epidermis at junction of hydranth body and caulus; asexual reproduction by transverse fission.

REMARKS: This is currently a monotypic genus.

Boreohydra simplex Westblad, 1937

Fig. 4

Boreohydra simplex Westblad, 1937: 1, figs 1-4; Westblad, 1947: 1-13, figs 1-4, pls 1-3; Nyholm, 1951b: 531, text fig., pl. 1 figs 1-4; Westblad, 1953: 351, figs 1-2; Prévot, 1959: 97, pl. 1 fig. 2; Calder, 1974: 1666, fig. 1; Bozhenova *et al.*, 1989: 11, fig.; Petersen, 1990: 148; Schuchert, 2001a: 36, fig. 23A-B; Bouillon *et al.*, 2004: 86, fig. 47L.

MATERIAL EXAMINED: See Schuchert (2001a).

DIAGNOSIS: Small, solitary, mud-dwelling hydroids with three to four capitate oral tentacles and scattered wart-like nematocyst clusters on hydranth body.

DESCRIPTION: Solitary hydroid, composed of hydranth body and conical peduncle. Hydranth spindle-shaped, hypostome short and rounded, surrounded by

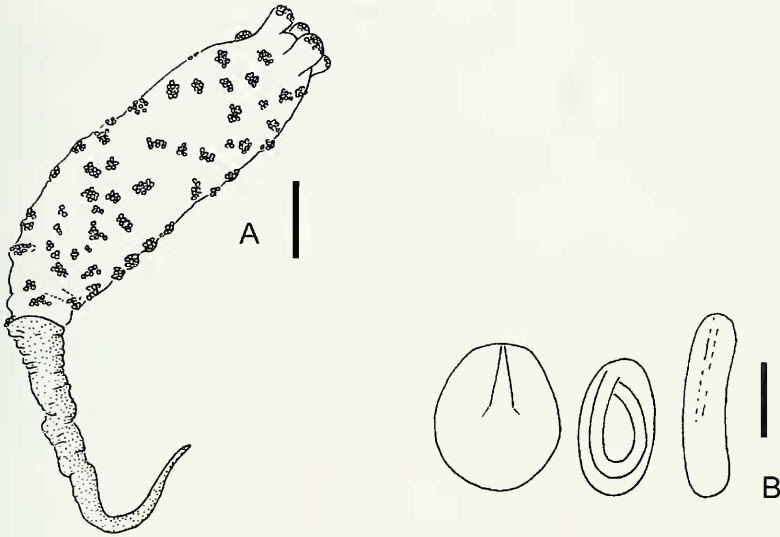


FIG. 4

Boreohydra simplex Westblad, 1937; Northern Greenland, Pearyland, after Schuchert (2001a). A) polyp, scale bar 0.2 mm. B) stenotele, desmoneme, isorhiza, scale bar 10 μ m

three to four short, stubby tentacles, only slightly capitate. On hydranth body 50-60 scattered nematocyst clusters, variable in size, 3-15 capsules per cluster, clusters slightly elevated and wart-like. Hydranth body at base tapering and turning into peduncle, peduncle conical, constantly tapering into fine tip at its end, covered by wrinkled perisarc. Gastrodermis with three or four longitudinal folds. Nematocysts: stenoteles; desmonemes, discharged with four coils; isorhizas.

DIMENSIONS: Hydranth body height 0.8-1.5 mm, diameter about 0.3 mm; peduncle 0.4-1 mm long. Nematocysts: stenoteles (17-19) \times (16) μ m; desmonemes, (16-17) \times (9-11) μ m; isorhizas (17-20) \times (4.5-5.5) μ m.

BIOLOGY: Fairly common in mud bottoms characterized by the '*Brissopsis lyrifera* - *Amphiura chiajei*' community (Petersen, 1913; Jones, 1950) at depths of around 40 m (Westblad, 1953). The depth range varies from a few metres to more than 600 m (Christiansen, 1972). The animal is able to move quite rapidly on the surface of mud (Hult, 1941). The latter author also described how it burrows into the mud. The oral tentacles are instrumental for this process. The food seems to be mainly composed of small nematodes (Westblad, 1947).

ADDITIONAL DATA: (Westblad, 1947; Nyholm, 1951b) The polyp multiplies by transverse fission and produces gonophore-like outgrowths without germ-cells. Eggs were found in the epidermis at the junction of the body and peduncle. Westblad (1947) gives further details on the variability: of 60 animals, 47 had three tentacles, the others four. The number of tentacles and the number of gastrodermal folds is not closely correlated. Prévot (1959) depicts a longitudinal section. Bozhenova *et al.*, (1989) depict the nematocysts and provide measurements.

DISTRIBUTION: Bipolar, northern and southern Atlantic Ocean in temperate to Arctic waters, probably quite frequent, but often overlooked. It was particularly often recorded along the Atlantic coast of Scandinavia. The southern limit for Europe is the English Channel. Recorded from the White Sea, Norway to Sweden, Great Britain, Iceland, North Greenland, North-Eastern Canada, North Greenland, South Georgia (Hult, 1941; Westblad, 1953; Christiansen, 1972; Calder, 1974; Bozhenova *et al.*, 1989; Schuchert, 2001a). Type locality: Tromsø and Ramfjord, Norway.

REMARKS: Westblad (1947) supplemented the first description by further anatomical and ecological details. He observed buds that he interpreted as gonophores, however he could not find germ cells in them. Later, Nyholm (1951) observed eggs in the epidermis and concluded that the germ cells of this species are not collected in sporosacs, but remain in the epidermis like in *Hydra*. Petersen (1990) interpreted the gonophore-like outgrowths observed by Westblad (1947) as incipient polyp buds. More work is needed to reveal the nature of these buds.

Genus *Psammohydra* Schulz, 1950b

TYPE SPECIES: *Psammohydra nana* Schulz, 1950b.

DIAGNOSIS: Solitary hydroids of very small size, living attached to sand grains; one whorl of filiform tentacles in middle region of hydranth; hypostome proboscis-like, with terminal swelling. Asexual reproduction through fission.

REMARKS: This is currently a monotypic genus. The sexual reproduction is insufficiently known.

Psammohydra nanna Schulz, 1950

Fig. 5

Psammohydra nanna Schulz, 1950b: 122, figs 1-9; Riedl, 1970: 153, pl. 43; Clausen, 1971: 2, fig. 1; Clausen & von Salvini-Plawen, 1986: 34, fig. 3; Thiel, 1988: 267, fig. 19.1d; Bouillon *et al.*, 2004: 87, fig. 48A.

MATERIAL EXAMINED: None, the type material could not be located.

DIAGNOSIS: Very small solitary hydroid living attached to sand grains, body skittle- to spindle shaped, one whorl of filiform tentacles in about middle of body.

DESCRIPTION: Tiny solitary hydroids, living attached to sand-grains; body shape and size very variable, usually skittle- or spindle-shaped, with flat base when attached, slightly above middle a single whorl of four (rarely 3-5) tentacles; hydranth body above tentacles proboscis-like, with terminal swelling. Proboscis movable and extensible, mouth terminal but invisible when not used. Tentacles short, straight, contractile, filiform, nematocysts evenly distributed, gastrodermis chordoid. Sexual reproduction insufficiently known, reportedly only one egg is produced. Colour: sand-grey. Nematocysts: stenoteles, desmonemes, atrichous isorhizas.

DIMENSIONS: Total body size 0.28-0.4 mm, but very variable, can contract or expand its body about two times. Nematocysts: stenoteles (6-7)x(5-6) μ m, isorhizas (5.5-6.8)x(2.3-3) μ m; desmonemes (3.5-5.5)x(2.3-3.5) μ m (Schulz, 1950b).

BIOLOGY: Vegetative reproduction takes place by transverse fission. The animal can move by creeping like a freshwater *Hydra*. It is a member of the meiofauna and

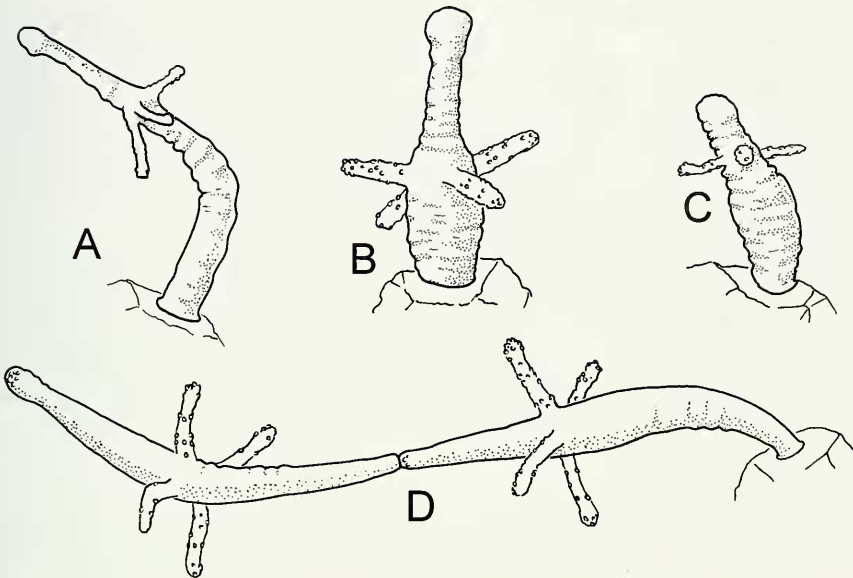


FIG. 5

Psammohydra nanna Schulz, 1950, redrawn from Schulz (1950b), no scale given. A-C) Animals on sand-grains in various states of contraction. D) Vegetative reproduction by transverse fission.

occurs in fine sand in shallow waters of a few metres. Schulz (1950b) characterizes the community where it was found as "*Turbanella hyalina*" community (Remane, 1933). It can tolerate reduced salinity down to 8‰ (Schönborn *et al.*, 1993).

ADDITIONAL DATA: Of 46 examined animals, 39 had four tentacles, four had three tentacles, and three five (Schulz, 1950b). Schulz (1950b) also describes the histology of this animal. The gastrodermal epithelium is high in the lower part of the animals, almost obliterating the lumen, but it is low above the tentacles and thus leaves a distinct cavity. The proboscis contains only stenoteles and isorhizas. The desmonemes are confined to the tentacles. The proboscis is very extensible and can bend to all sides. It acts like a central tentacle and it is used for locomotion and food capture. Swedmark (1959) mentions without further comment that *Psammohydra* produces a single egg only.

DISTRIBUTION: Western Baltic Sea (Schulz, 1950b), English Channel (Teissier, 1965); western Mediterranean (Swedmark, 1956), Adriatic Sea (Salvini Plawen, 1966).

REMARKS: The taxonomic position of this simplified animal is unclear (see also remarks for family Acaulidae and Boreohydridae).

FAMILY PROTOHYDRIDAE Allman, 1888

TYPE GENUS: *Protohydra* Greeff, 1869.

DIAGNOSIS: Solitary, small, elongated hydroids usually living in brackish-waters; without tentacles and gonophores, pedal disc formed by epidermal cells only;

gametes bulging into gastric cavity, nematocysts: stenoteles and isorhizas, evenly distributed over body.

Genus *Protohydra* Greeff, 1869

TYPE SPECIES: *Protohydra leuckarti* Greeff, 1869.

DIAGNOSIS: With the characters of the family.

REMARKS: Due to their – likely secondary – very simple morphology, the Protohydridae are difficult to classify. Petersen (1990) treated the family as *Capitata incerta sedis*. The cnidome is quite interesting as it lacks desmonemes. This could, however be due to the absence of tentacles. In *Psammohydra nanna*, a similarly reduced form, the desmonemes are associated with the tentacles. The family currently comprises two species: *Protohydra leuckarti* Greeff, 1869 and *Protohydra psamathe* Omer-Cooper, 1964. *Protohydra caulleryi* Dawydoff, 1930, characterized by budding or frustules, is likely a polyp belonging to the Oliandiasidae (Weill, 1935; Schulz, 1952).

Protohydra leuckarti Greeff, 1869

Fig. 6

Protohydra leuckarti Greeff, 1869: 37, pls 4-5; Luther, 1923: 1, figs 1-11; Koller, 1927: 97, figs 1-2; Westblad, 1930a: 1-4; Westblad, 1930b: 1-13, figs 1-3; Weill, 1934: 448; Weill, 1935: 83, fig. 5; Westblad, 1935: 152, figs 1-4; Vervoort, 1946: 47, fig. 1; Schulz, 1950a: 53; Nyholm, 1951a: 529, pl. 1; Naumov, 1969: 593, fig. 439; Clausen, 1971: 1.

MATERIAL EXAMINED: ZMUV, Denmark, Mariagerfjord, Ajstrupbugt, 0.5 m, 31 July 1955, 3 specimens, det. Kramp. – IRSN, two samples from Roscoff, collected by J. Bouillon in May 1964 (many specimens) and August 1961 (few specimens).

DIAGNOSIS: Solitary, small, elongated hydroids without tentacles and gonophores, gametes bulging into gastric cavity; vegetative reproduction usually by transverse fission or rarely by lateral buds; nematocysts: stenoteles and isorhizas.

DESCRIPTION: Solitary, brackish-water hydroids, usually elongate spindle- to club-shaped when relaxed, spherical when contracted. Tentacles absent, at aboral end a small epidermal attachment disc for temporary attachment, no perisarc, nematocysts evenly distributed in epidermis, not concentrated around mouth. Vegetative reproduction by transverse fission, rarely by buds (Schulz, 1952). Gonophores absent, gametes differentiate from epidermal cells and proliferate into gastric cavity where the gonad remains attached along one side of the body wall, gonochoristic, females produce one egg only which is expelled by perforation of the body wall. Nematocysts (Luther, 1923; Weill, 1934; Schulz, 1950b): stenoteles and basitrichous isorhizas, desmonemes absent.

DIMENSIONS: Adults maximally contracted to a sphere 0.4 mm, expanded 2-3 mm (Greeff, 1869). Eggs ca. 0.25 x 0.14 mm (Westblad, 1930b). Nematocysts (Luther, 1923): stenoteles 12-17 µm long, isorhizas (7)x(3-3.5)µm,

ADDITIONAL DATA: There are pigment granules of variable size in the gastrodermis. The colour of the animals depends on the food items and is either colourless or various shades of red (Greeff, 1869; Madsen, 1939). Westblad (1935) showed that the germ cells originate from epidermal cells that proliferate into the gastric cavity. The animals are gonochoristic and females produce a single egg. The egg is expelled by a

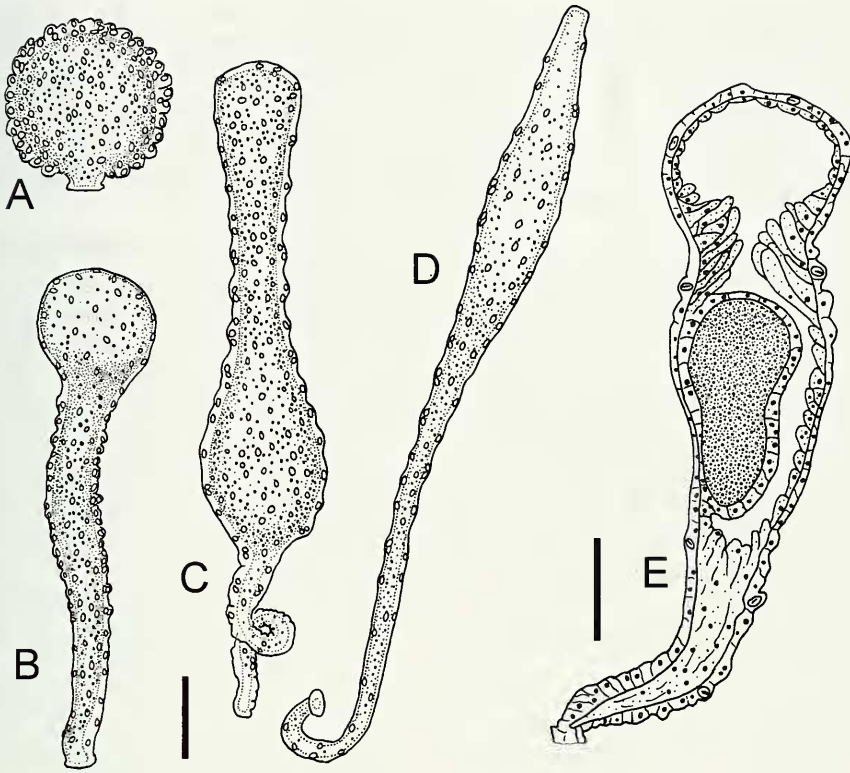


FIG. 6

Protohydra leuckarti Greeff, 1869. A-D) Animal in various states of contraction, oral end upwards, scale bar approximately 0.2 mm, redrawn from Greeff (1869). E) Schematic longitudinal section of male animal, the gonads (stippled) bulge into the stomach lumen, scale bar 0.1 mm, redrawn from Westblad (1935).

rupture of the body wall and the animal dies afterwards. Westblad (1935) also made some observations that hint at a possible copulation. This is rather exceptional for hydrozoans and needs reconfirmation. Schulz (1952) observed that besides the usual transverse fission, rarely some animals produce lateral polyp buds. Further biological data are also provided by Muus (1966) and Wehling (1978). Some information on the histology – e. g. the body wall, the glue cells, and gametogenesis – are provided by Luther (1923) and Westblad (1935).

BIOLOGY: A coastal, euryhaline species occurring in brackish waters of wave protected habitats, often in closed bays, estuaries, and lagoons. It is absent from agitated waters. The depth range is from a few cm to about 20 m and the reported salinity range 0.38-30‰ (Westblad, 1930a; Madsen, 1939; Schulz, 1950a; Schönborn *et al.*, 1993, Barnes, 1994). Various bottom types have been reported, but there seems to be a preference for fine sand or mud with much detritus. They can reach very high densities, reaching from 1000 individuals per square metre in winter to 50'000 in

summer, or even exceptionally 200'000/m² (Heip, 1971). Rarely it also occurs on algae. It can be found all year round, but reaches maximum densities in summer when it also gets sexually mature. *Protohydra leuckarti* is an important predator in its biotope and it regulates the density of other animals (Heip, 1971; Heip & Smol, 1976). The animal is able to creep and to burrow. It lives on a variety of food items, especially nematodes, copepods, ostracods, chironomid larvae (Schulz, 1950a). It is preyed upon by e. g. nudibranchs (Evertsen *et al.*, 2004).

DISTRIBUTION: Circumglobal in temperate brackish waters of the northern hemisphere. The northern limit in Europe is southern Norway (Oslofjord: Christiansen, 1972) and southern Finland (Helsinki: Schneider, 1927). It has been reported from the Atlantic coast of Sweden (Westblad, 1930a); the Baltic Sea (Schneider, 1927; Westblad, 1935; Koller, 1927; Nyholm, 1951; Schulz, 1950a); Denmark (Madsen, 1939; Muus, 1966; Rasmussen, 1973); German part of the North Sea (Schulz, 1950a); Holland (Boaden, 1976); Belgium (Greeff, 1869; Heip, 1971); Southern England (Baker, 1913; Hickson, 1920); Brittany (Teissier, 1965); Bay of Biscay (Nyholm, 1951a); in the Mediterranean it was found in brackish water lakes of southern France (Nyholm, 1951a). It has also been found in the Black Sea (Valkanov, 1947; Marcoci, 1956). Outside Europe it has been recorded on the east coast of North America (Ruebush, 1939), in the north-eastern Pacific (Wieser, 1958), the north-western Pacific (Naumov, 1969), and the Aral Sea (Maier, 1974). Type locality: Ostende, in mud among oyster cultures.

FAMILY CANDELABRIDAE STECHOW, 1921

TYPE GENUS: *Candelabrum* de Blainville, 1830: 284.

SYNONYMS: Myriothelidae Hincks, 1868; Symplectaneidae Fraser, 1941.

DIAGNOSIS: Large, worm-like hydroids, solitary or forming small pseudo-colonies through connected aggregates, attached to substrate but without stolons; hydranth elongated, cylindrical to club-shaped; with numerous scattered, hollow or parenchymatic capitate tentacles, tentacles simple or compound, if compound then with adnate basal parts. Hydrocaulus with or without perisarc, with tentacle- or root-like attachment-processes. Gonophores fixed sporosacs, developing either directly on hydranth body or on club-shaped blastostyles.

REMARKS: Stechow (1921: 248) pointed out that the genus *Candelabrum* de Blainville, 1830 has priority over *Myriothela* Sars, 1850. Consequently, he then also changed the family name from Myriothelidae Hincks, 1868 to Candelabridae Stechow, 1921. According to the ICZN [4th ed. 1999, 40.2] such a name change is valid if it was made before 1961 and if the new name has been widely used. The name Candelabridae has only recently come into usage (e. g. Bouillon, 1985; Schuchert, 1996; Hewitt & Goddard, 2001), while other used Myriothelidae (e. g. Calder, 1972; Millard, 1975; Petersen, 1990). I therefore suggest that for the sake of nomenclatural stability, Candelabridae should be used from now on. This name matches the genus name and it is also used in several large electronic databases. If in future Candelabridae should not become the prevailing name, then a ruling of the International Commission on Zoological Nomenclature must be requested.

The family currently comprises the following genera: *Candelabrum* de Blainville, 1830; *Monocoryne* Broch, 1910, and *Fabulosus* Stepanjants, 1990.

KEY TO THE GENERA:

- 1a capitate tentacles simple 2
 1b capitate tentacles compound *Monocoryne*
 2a sporosacs borne on blastostyles *Candelabrum*
 2b sporosacs borne singly on hydranth body *Fabulosus* (not in European fauna)

Genus *Candelabrum* de Blainville, 1830

TYPE SPECIES: *Lucernaria phrygia* Fabricius, 1780 = *C. phrygium* (Fabricius, 1780).

SYNONYMS (after Segonzac & Vervoort, 1995): *Arum* Vigurs, 1850; *Myriothela* M. Sars, 1850; *Spadix* Gosse, 1853a; *Acandela* Stechow, 1920.

DIAGNOSIS: Solitary hydroids or loose aggregates comprising few polyps that may have a common perisarc base. Hydranth long, cylindrical or club-shaped, upper part with numerous simple capitate tentacles; at base a foot region, with or without perisarc sheath, with attachment processes that are either covered with perisarc or naked and may have a perisarc disc at their end; gonophores are fixed sporosacs borne on blastostyles developing in region between tentacles and foot. With or without clasper tentacles that hold developing embryos. Development direct, leading to young polyps without a planula stage.

REMARKS: Segonzac & Vervoort (1995) recently revised the genus *Candelabrum*, outlining its synonymy and taxonomic history.

KEY TO THE NORTH-ATLANTIC *CANDELABRUM* SPECIES:

- 1a sporosacs without nematocyst buttons 2
 1b sporosacs with nematocyst buttons *C. verrucosum*
 2a foot large, covered by perisarc sheath, hermaphroditic 3
 2b foot without perisarc sheath, without clasper tentacles, dioecious, deep water or Arctic form *C. phrygium*
 3a boreal shallow water form, with clasper tentacles holding developing embryos *C. cocksii*
 3b deep water form, without clasper tentacles *C. serpentarii* (not in European fauna)

Candelabrum cocksii (Cocks, 1854)

Fig. 7

Arum Cocksii Vigurs, 1850: 90, *nomen nudum*.

Spadix purpurea Gosse, 1853a: 126; Cocks, 1853: 365.

Spadix cocksii – Gosse, 1853c: 386.

Arum cocksii Cocks, 1854: 34, pl. 3, fig. 7-12.

Myriothela phrygia – Hincks, 1868: 77, pl. 12 fig. 3; Allman, 1874: 317; Hardy, 1891: 505, pls 36-37; Hartlaub, 1916: 110, figs 38-39.

[not *Candelabrum phrygium* (Fabricius, 1780)]

Myriothela – Allman, 1876: 549, pls 55-58 [only named *Myriothela phrygia* in plates].

Arum cocksii – Rees, 1957: 487, figs 37 & 39A-B; Prévot, 1959: 97, pl. 1 fig. 1.

Myriothela cocksii – G. O. Sars, 1874: 130; Bonnevie, 1899: 36; Billard, 1921: 12, fig. 1; Weill, 1934: 373; Manton, 1941: 143, figs 1a-b, 2.

Candelabrum cocksii – Segonzac & Vervoort, 1995: 37, fig. 2c-d, table 1.

MATERIAL EXAMINED: MHNG INVE 36299, France, Roscoff, near Ile Verte, 0 m, 17 September 2004, 3 specimens, fertile, examined alive, one blastostyle used for serial histological sections, confirming the presence of two male sporosacs and several female ones. – MHNG INVE 29591, France, Roscoff, near Île Verte, 0 m, 30 March 1998, 2 specimens,

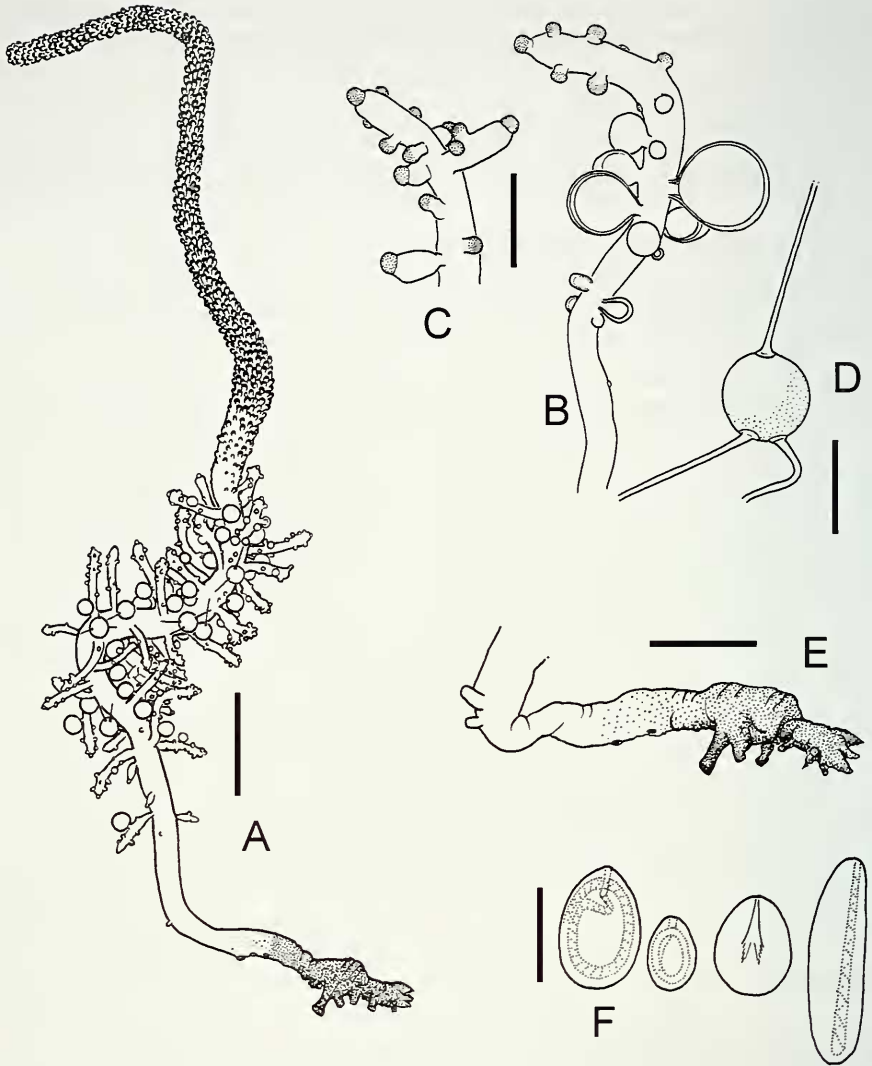


FIG. 7

Candelabrum cocksii (Cocks, 1854); A, after photographs of living animals, C-F, after preserved material. A) Entire polyp, semi-extended, capitate tentacles contracted, scale bar approximately 5 mm. B) Blastostyle with sporesacs and capitula (stippled), scale bar 1 mm. C) Tip of blastostyle with branched end, same scale as B. C) Embryo held by three clasper tentacles, scale bar 1 mm. E) Attached base of hydranth, perisarc dark, note two small perisarc discs in lighter region, scale bar 3 mm. F) Nematocysts of mature polyp: large and small desmonemes, stenotele, microbasic eurytele, scale bar 10 μ m.

attachment part lacking, fertile, 28S sequence of this material in GenBank under accession number AY920796, 18S AY920758, 16S AY787879. – MHNG INVE 35726, France, Roscoff, Tyaozon, 6 May 1910, coll. M. Bedot. – BMNH 1980.3.1.1, misidentified as *Candelabrum phrygium*, England, Devon, Salcombe, Castle Rock, 19 Feb 1980, R. L. Manuel, 3 well preserved specimens, eggs held by claspers present, base in irregular perisarc.

DIAGNOSIS: *Candelabrum* species with clasper tentacles that hold embryos, hermaphroditic, base long and sheathed in perisarc envelope that is adnately attached to the substratum.

DESCRIPTION: Solitary, relatively large, firmly attached, worm-like polyps, divided into three regions: foot, blastostyle region in middle, and trunk.

Foot large, about 1/4 to 1/3 of whole animal, bent horizontally so that attachment to substrate is adnate, basal region encased in firm, brown perisarc, distorted and gnarled to fit irregularities of the substratum and provided with short, lobed or finger-like projections with flat ends adhering to the solid substratum; the perisarc gradually thins out distally; on thinner perisarc region there can be a few thick, sharply demarcated perisarc discs used for attachment, but without being associated with notable protrusions of the hydranth wall; further distal some short finger-like protrusions of the hydranth wall can occur.

Blastostyle region of about the same length as foot, provided with numerous (>20-40), widely spaced blastostyles bearing the gonophores and with thin clasper tentacles holding embryos. Blastostyles contractile, hollow and lumen in connection with gastric cavity, stick- to club-shaped (swollen distally), sometimes branched in distal region, distal region provided with nematocyst clusters, these in hemispherical bumps or stubby capitate tentacles with short thick pedicels, quite irregular in appearance; proximal 2/3 of blastostyle with irregularly scattered gonophores, different developmental stages mixed. Gonophores are fixed sporosacs without radial canal system (cryptomedusoid type); males and females occurring on same blastostyle, the animals are thus simultaneous hermaphrodites. Sporosacs spherical, white, female ones larger than male ones, females initially with numerous small oogonia but ultimately only one egg matures. Mature or fertilized eggs leave sporosac but are then grasped by two to five clasper tentacles. Clasper tentacles thin, straight, of variable length, originating in pairs or more at bases of blastostyles or also independently of them, without nematocysts, terminal region sucker-like, enlarged, and attached to the envelope of developing eggs.

Trunk region comprising about half of the animal, capable of great expansion and strong contraction, elongate club-shaped with largest diameter following the blastostyle region, evenly and entirely covered by hundreds of imbricate, indistinctly capitate tentacles; capitate tentacles contractile, hollow, pedicel short in material taken out of the sea (even when anaesthetized, but can extend considerably in undisturbed specimens and become distinctly capitate), capitulum ovoid, diameter not much larger than the contracted pedicel.

The foot and blastostyle parts are less contractile than the trunk. In animals which have been preserved without relaxation, the trunk region is thus only as large or smaller than either the foot and blastostyle region. The long foot is characteristic for this species (comp. Figs 7 and 8-9).

Nematocysts of mature animals: two types of desmonemes, stenoteles, microbasic euryteles. In young polyps, there are also isorhizas (Weill, 1934); they may also be found rarely in adults (own observations).

Colours: living animals entire body, blastostyles, and sporosacs white, capitula of tentacles of trunk purple, perisarc dark amber-brown.

DIMENSIONS: Mature body size variable and difficult to establish due to great contractibility, ranging from a few cm to 12 cm, reportedly also more, usually 2-3 cm when contracted; blastostyles up to 4 mm but contractile; capitula of trunk tentacles diameter about 0.2 mm, expanded tentacles up to 2 mm long (Allman, 1874); clasper tentacles 1-2 mm long; diameter of fertilized eggs held by claspers 0.7-0.8 mm, female sporosacs reach same diameter; male sporosacs smaller, 0.30-0.42 mm (Segonzac & Vervoort 1995). Nematocysts of mature animal (preserved material, see Fig. 7F): large desmonemes (12-14) \times (8.5-9.5) μ m; small desmonemes (7.5-9) \times (5-6) μ m; stenoteles (11-11.5) \times (8-9) μ m; microbasic euryteles (18-20) \times (5.5-6) μ m, ratio of everted shaft to capsule length around 0.9; presumed isorhiza 13.5 \times 5 μ m.

BIOLOGY: Along the coasts of Brittany, fertile animals have been documented from January to September (Teissier, 1965; Castric-Fey, 1970, own data), but likely some animals are reproductive all year round. Asexual reproduction may take place by budding small polyps at the junction of the foot and blastostyle region (Hardy, 1891; Hartlaub, 1916). This asexual budding takes place before the onset of sexual reproduction in early spring (Hardy, 1891).

The animals occur at the spring tide low-water-mark, but records down to 17 m are known (Castric-Fey, 1970; Segonzac & Vervoort, 1995). Sars (1874) gives a depth of 110-146 metres for his record from the Aalesund, which is unusually deep for this animal. Intertidally, the species occurs attached on the underside of large boulders. They can also be attached to holdfasts of laminarians (Castric-Fey, 1970). Billard (1921) made some preliminary observations on their feeding biology. With their much extensible trunk they search their surroundings for small benthic amphipods. It takes about five to six hours to digest one of them. The animals are also able kill shrimps of up to 2 cm size.

The embryonic development takes place in the embryonic envelope that is held by the clasper tentacles. The animal can thus be considered an actively brooding species. The clasper tentacles only attach to fertilized eggs, as only these form the necessary embryonic envelope (Beigel-Heuwinkel, 1988). The development results in a young polyp with 17-22 tentacles (Billard, 1921). The primary tentacles of the young polyp are only transitory and are replaced by permanent tentacles. More details on the development are given in Allman (1876, as *Myriothela*), Billard (1921), Benoît (1923a, 1925), and van der Vyver (1968).

ADDITIONAL DATA: The gastrodermis has numerous folds and villi (cylindrical projections), but has no compartmentalization as in the Tubulariidae (Allman, 1876). The mesogloea is massive and contains thick fibres (Beigel-Heuwinkel, 1982a). It is also involved in the attachment to the substratum (Manton, 1941). Histological details can be found in Allman (1876, as *M. phrygia*) and Hardy (1891, as *M. phrygia*). The tentacles are hollow. Prévot (1959) shows them as closed off to the gastric lumen by a mesogloea lamella, but Allman (1876, pl. 56, fig. 2) states that they are open. An examination of some hand-made cross-sections of the available material showed that there are indeed small openings, but this should be corroborated by more reliable evidence obtained by serial histological sections. The strong contractibility of the tentacles may be regulated by the hydrostatic pressure of the water in the lumen of the

tentacles. If so, an opening to the stomach seems more understandable. The initial tentacles formed while the embryo is still in the egg capsule develop towards the gastric lumen and are only everted at a later stage (Allman, 1876). The primary tentacles must thus have a basal opening. The primary tentacles are quite long and replaced after hatching by shorter tentacles (Allman, 1876).

The sporosacs and their development have been examined by Allman (1876, as *M. phrygia*), Korotneff (1888), Hardy (1891, as *M. phrygia*), Benoît (1923b), and Beigel (1976). Manton (1941) studied the foot and the clasper tentacles. The clasper tentacles were also investigated by Beigel-Heuwinkel (1988). She used light and electron microscopic data to show that the cells at the tip secrete a substance that acts to glue the claspers to the embryonic envelope. Unfertilized eggs do not form an embryonic envelope and are thus not held by the claspers.

Results of regeneration experiments were reported by Billard (1921) and Beigel-Heuwinkel (1982b). Regenerating upper halves of a polyp form no perisarc sheath, but anchoring tentacles as in *C. phrygium*.

DISTRIBUTION: North-Eastern Atlantic, absent from the North Sea, Baltic Sea, Mediterranean and Black Sea. The northernmost record is Norway (Aalesund, G. O. Sars, 1874; somewhat doubtful, needs reconfirmation), common in the western English Channel coast of Great Britain and France, also recorded from the Scilly Islands, Isle of Man, western England, southern Brittany, Galicia, Bay of Cadiz (southernmost record) (Segonzac & Vervoort, 1995, Medel & López-González, 1996, this study). Type locality: Gyllyngvase, (Gwyllyn-vase in Cocks, 1850), Falmouth, Cornwall, United Kingdom.

REMARKS: *Candelabrum cocksii* has usually been attributed to Vigurs (1849), but that is incorrect. The binomen *Arum cocksii* was introduced in a paper by Cocks that almost certainly appeared in 1850 and not 1849 (Cornelius, 1977). Cocks attributed the name to Vigurs without providing a description. It is thus an invalid name (*nomen nudum*). Furthermore, it seems that Cocks initially did not recognize it as a hydrozoan as he placed it among the Sipuncula. Gosse (1853a: 126) then published the name *Spadix purpurea*, of which Cocks (1853: 365) acknowledged in the same journal that it is identical to his *Arum cocksii*. Cocks (1853) used *Spadix purpurea* as species name followed by *Arum cocksii* in brackets to formalize the synonymy. A suitable description and figures of *Arum cocksii* followed shortly afterwards in Cocks (1854), which made the name formally available for the first time [ICZN, 1999, 4th ed., 50.1] [the publication date of Cocks's paper is somewhat unclear, it could be 1853 or 1854; according to Cornelius (1977) it was likely 1854]. Gosse (1853c: 386) acknowledged the synonymy and he apparently ceded his species designation to Cocks by the footnote ".....I gladly recognise, however, the superior claim [of Cocks] of the specific appellation, which pays a deserved compliment to an excellent naturalist."

Although *Spadix purpurea* Gosse, 1853 is likely a senior synonym of *Arum cocksii* Cocks, 1854, the combination *Candelabrum cocksii* (Cocks, 1854) must be taken as valid, this because to my knowledge Gosse's name has not been used as valid after 1899 [ICZN, 1999, 4th ed., 23.9.1.1], while *C. cocksii* has been used regularly (see Vervoort & Segonzac, 1995).

Candelabrum cocksii (Cocks, 1854) has unfortunately been confounded with *C. phrygium* (Fabricius, 1780) by Hincks (1868), Allman (1876), and many subsequent authors relying on Hincks (see Vervoort & Segonzac (1995) for synonymy and misidentifications). Recently, Cornelius (1977) again maintained that both are conspecific. Cornelius based his claim by referring to other authors, e. g. Stechow (1923) and Teissier (1965). These two authors, however, do not claim such a synonymy, and Stechow even advocates a separation at the genus level. The opinion of Cornelius is also not shared by Segonzac & Vervoort (1995) as well as by the present author. Both species are clearly separable. *Candelabrum cocksii* and *C. phrygium* differ in the foot morphology (long, perisarc covered foot versus short, naked one); clasper tentacles (presence versus absence), and the sexual reproduction (hermaphroditic versus gonochoristic).

The tentacles of the trunk are usually short and only indistinctly capitate, this in preserved material as well as in living material taken into the laboratory. The tentacle pedicels are very contractile and undisturbed animals have quite long tentacles (2 mm; Allman, 1874). This has also been observed for the closely related species *C. serpentarii* (see figs 3A-B in Segonzac & Vervoort, 1995). *Candelabrum serpentarii* Segonzac & Vervoort, 1995 is only known from deep waters of the central Atlantic. This species is also monoecious, but lacks clasper tentacles and its eggs are four to five times larger. The only *Candelabrum* species that also has clasper tentacles is the Pacific *Candelabrum fritchmanii* Hewitt & Goddard, 2001. This species can form colony-like aggregates, a unique feature within this genus.

Candelabrum phrygium (Fabricius, 1780)

Fig. 8

Lucernaria phrygia Fabricius, 1780: 343.

Myriothele arctica M. Sars, 1850: 14.

Myriothele phrygia – Sars, 1877: 23, pl. 2 figs 29-36; Bonnevie, 1899: 35, pl. 4 figs 5-6; Jäderholm, 1908: 9, pl. 1 fig. 7; Broch, 1916: 19, fig. C, pl. 1 figs 3 & 8; Rees, 1957: 486, fig. 36; in part Naumov, 1969: 261, not figures; Calder, 1972: 222, pl. 1 fig. 5.

? *Myriothele gigantea* Bonnevie, 1898a: 490, pl. 27 figs 46-47; Bonnevie, 1899: 38, pl. 4 fig. 1.

? *Myriothele minuta* Bonnevie, 1898a: 489, pl. 27 fig. 44; Bonnevie, 1899: 37, pl. 3 fig. 6a-b, pl. 4 fig. 4.

? *Myriothele mitra* Bonnevie, 1898a: 489, pl. 27 fig. 43; Bonnevie, 1899: 38, pl. 3 fig. 6c-e, pl. 4 fig. 3.

Candelabrum phrygium – in part Cornelius 1977: 521 [excl. synonymy]; Segonzac & Vervoort, 1995: 45, figs 2e-f, 3E-F, table 1 [some references do not refer to this species]; Schuchert, 2001a: 37, fig. 24.

MATERIAL EXAMINED: Re-examined material mentioned in Schuchert (2001a), ZMUC, Greenland, no exact locality and date known, collected by Lüthken, identified by P. Kramp, two specimens, both broken into two parts, one obvious female on branching bryozoan (Cellariidae), other animal on red algae, previously identified as male; one blastostyle of both specimens was used for serial histological sections, both specimens proved to have female sporosacs only, though the tissue preservation is not good. – All suitable material found in the BMNH that is labelled as *C. phrygium* turned out to be *C. cocksii*.

DIAGNOSIS: *Candelabrum* species without clasper tentacles, dioecious, basal foot short or absent, straight and not sheathed in perisarc envelope, attached to substratum by tentacle-like filaments usually ending in perisarc discs.

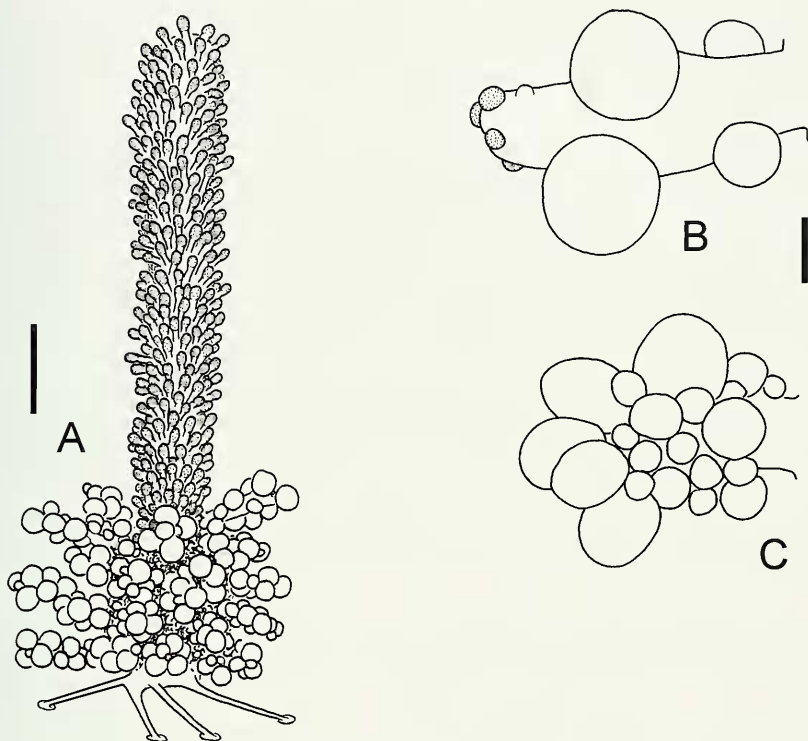


FIG. 8

Candelabrum phrygium (Fabricius, 1780), after preserved material from Greenland. A) Entire polyp, scale bar 2 mm. B-C) Blastostyles, scale bar 0.5 mm.

DESCRIPTION (after Sars, 1877; Segonzac & Vervoort, 1995; own data): Polyp solitary, worm-like, size very variable as able to expand and contract enormously. Hydranth shape also variable, usually cylindrical to conical, subdivided into a distal tentaculate region (trunk), followed by a blastostyle region and sometimes also a foot zone.

Foot zone either very short in relation to other parts or absent, not curved, adhering to substratum by several tentacle-like attachment filaments, each of them with terminal region sucker-like and enlarged, attached to a perisarc disc that adheres to substratum, perisarc discs sometimes absent.

Blastostyle region about 1/4 to 1/3 of contracted polyp, beset by many (>20) club-shaped blastostyles. At distal end of blastostyles four to six nematocyst clusters in wart-like tubercles. Blastostyles bear sessile sporosacs, the two sexes on different polyps, sporosacs without nematocyst tubercles. Male sporosacs spherical, without radial canals, up to 50 per blastostyle at different developmental stages. Females with two to six sporosacs per blastostyle, maximally two mature, others in development, spherical, no radial canals, initially many eggs but presumably only one egg per sporosac attains maturity, fertilized in situ and developing into a young polyp, hence viviparous.

Trunk region comprising majority of hydranth length, with numerous (>200) capitate tentacles, these hollow, extensible, capitula ovoid.

Colours: cream-white. Nematocysts: stenoteles; ? haplonemes; desmonemes of two size classes.

DIMENSIONS: Height of contracted specimens 2-6 cm, expanded up to 30-40 cm (Bonnievie, 1899; Broch, 1916), width a few mm. Diameters of male sporosacs 0.4-0.8 mm when mature, females 0.9-1.4 mm. Capitate tentacles with stalk 0.3-0.5 mm, capitula 0.17-0.25 mm (Segonzac & Vervoort, 1995). Nematocysts (Segonzac & Vervoort, 1995): stenoteles (10.6-11.5)x(8.2-9.8) μm ; ? haplonemes (19.7-20.5)x(8.2-9.9) μm ; desmonemes of two size classes (12.5-13.0)x(9.0-9.8) μm and (8.2-9.0)x(6.4-6.6) μm .

BIOLOGY: Occurs usually at considerable depths of several hundreds of meters down to 2195 m (Bonnievie, 1899), but in the high Arctic it has been found as shallow as 13 m (Jäderholm, 1908). The polyps live permanently attached to solid substrata like rock, bivalves, hydroids, bryozoans, and algae. The animals are viviparous and lack a planula phase (Sars, 1877; Schuchert, 2001a); the newly released polyp is spherical and has 20-30 capitate tentacles. The tentacles formed while the embryos are still in the egg capsule develop inverted into the gastric lumen, but evert before hatching.

DISTRIBUTION: An Arctic, deepwater species penetrating into boreal regions, in European waters reaching as far south as the Trondheimfjord and the Wyville-Thomson-Ridge between Scotland and The Faeroes (Broch, 1903; Broch, 1916). Segonzac & Vervoort (1995) report a find from the Mid-Atlantic Ridge south-west of the Azores in a depth of 1622 m, which is the southernmost record of this species. It has also been recorded in northern Norway (Sars, 1877; Bonnievie 1899), Jan Mayen (Broch, 1916), Russian Arctic Seas (Jäderholm, 1908; Naumov, 1969), northern Pacific (Naumov, 1969). Also known from Iceland (Broch, 1916), Greenland (Schuchert, 2001a), Canada (Calder, 1972). (Note that numerous other records under this name from coastal regions of the NE Atlantic refer in fact to *Candelabrum cocksii*). Type locality: Greenland.

REMARKS: The synonymy of this species has been worked out quite thoroughly (Sars, 1877; Bonnievie, 1899; Segonzac & Vervoort, 1995). *Myriothele arctica* Sars, 1850 was synonymized by Sars himself after he had re-examined Fabricius' type material (Sars, 1877). The boreal shallow-water species *Candelabrum cocksii* has often been synonymized with this species, but this is not tenable (see under *C. cocksii*). Some of Bonnievie's *Candelabrum* species (*C. minutum*, *C. mitra*, *C. giganteum*) are not well characterized and might also belong to this species (Rees, 1956). They are here listed as questionable synonyms (see also Segonzac & Vervoort, 1995). The material on which these three species were based, already fragmentary when examined by Bonnievie (1899), is now in such a bad condition that it is virtually useless (Rees, 1956). Contrary to the view of Rees (1956), *Candelabrum verrucosum* (Bonnievie, 1898) is well characterized and it is re-described below.

Candelabrum phrygium is portrayed as being dioecious, but for preserved material it is often difficult or impossible to determine the sex. This is easy only for

well advanced female sporosacs as they contain young polyps. For a reliable sex determination, serial histological sections must be made. One blastostyle of each of the two specimens examined for this study was thus used to make serial sections. Both animals had female sporosacs only. One specimen did not have sporosacs with advanced embryos and was thus initially mistaken for a male (Schuchert, 2001a). This shows that sex identifications of preserved material are often unreliable. More investigations using histological sections of entire blastostyles are desirable to confirm that *C. phrygium* is always dioecious (comp. *C. verrucosum*).

The material examined in this study and also by other authors (Sars, 1877) had attachment tentacles that were cemented to the substratum by distinct perisarc discs that adhere tightly to the substratum and cannot be removed without destroying them. Dislodged hydranths lack them regularly. Sometimes they are quite thin and inconspicuous and if attached on rock they might be hardly visible. This could explain that some investigators did not find them (e. g. Segonzac & Vervoort, 1995), but is well possible that they can also be absent.

***Candelabrum verrucosum* (Bonnevie, 1898)**

Fig. 9

Myriothela verrucosa Bonnevie, 1898a: 468, pl. 27 fig. 45; Bonnevie, 1899: 37, pl 4, fig. 2.
Candelabrum verrucosum – Segonzac & Vervoort, 1995: 53.

MATERIAL EXAMINED: ZMUC, Kap Farvel expedition station 148, 60.07°N 43.20°W (Greenland), 50 m, 27 August 1966, from rocky bottom, fertile female with sporosacs containing embryos, tissues somewhat shrunken. Two blastostyles were used to make serial histological sections, confirming the presence of male and female sporosacs.

DIAGNOSIS: *Candelabrum* species with sporosacs bearing scattered nematocyst buttons on their surface, monoecious, no clasper tentacles; foot straight, not covered by perisarc, attached via attachment filaments; size 1-4 cm.

DESCRIPTION (after examined specimen): Solitary polyp, 1.1 cm, cylindrical, divided into three regions: distal tentaculate region (trunk), followed by a blastostyle region and a foot zone.

Foot zone about 1/6 of animal, straight, with several (>10) tentacle-like attachment filaments of variable length, some of them with enlarged, sucker-like ends; one filament with terminal perisarc disc, those of other filaments presumably lost.

Blastostyle region taking up about half of the polyp, bearing many (>20) club-shaped blastostyles, clasper tentacles absent. Nematocyst clusters in wart-like tubercles at distal end of blastostyles. Blastostyles bear several (up to 8) sessile sporosacs. Sporosacs with up to eight distinct nematocyst buttons on surface, no radial canals or ring canals present. Largest sporosacs contain a single young polyp, animal thus viviparous. Besides female sporosacs, there is also one male sporosac per blastostyle, animals thus simultaneous hermaphrodites.

Trunk region about 1/3 of hydranth length, covered by numerous (>100) capitate tentacles, their capitula ovoid.

Nematocysts (not well preserved): stenoteles, large desmonemes, ? heteronemes.

DIMENSIONS: Hydranth can reach 4 cm (Bonnevie, 1898a), sporosacs up to 0.9 mm, blastostyles up to 2.2 mm, diameter of capitula 0.2 mm.

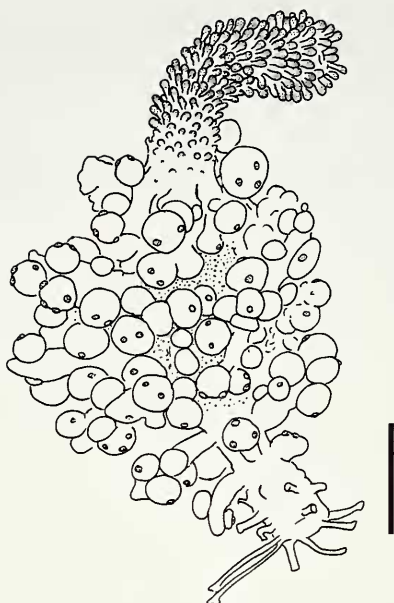


FIG. 9

Candelabrum verrucosum (Bonnievie, 1898), after preserved material from Greenland. A) Whole animal, the blastostyle region covers slightly more than half of the animal, note the nematocyst buttons on the sporosacs, scale bar 2 mm.

ADDITIONAL DATA: The tentacles formed while the embryos is still in the egg capsule develop inverted into the gastric lumen, but evert before hatching.

DISTRIBUTION: Northern Norway, Southern Greenland (this study). Type locality: Norway, Hammerfest (Bonnievie, 1899).

REMARKS: *Candelabrum verrucosum* (Bonnievie, 1898) has hitherto been known from one specimen described by Bonnievie (1898a, 1899). Some authors doubted its validity and thought it might belong to *C. phrygium* (e. g. Rees, 1956). The species is characterized by sporosacs that bear scattered buttons of nematocyst clusters. This is quite a unique feature and has never been observed for *C. phrygium*. I am convinced that *C. verrucosum* is a valid species, distinct from *C. phrygium*, and that the material described above belongs to it. The characteristic nematocyst buttons on the sporosacs are quite conspicuous in material examined with a dissecting microscope. There are a few discrepancies from the original material described by Bonnievie (1898a): there are more than two sporosacs per blastostyle, the blastostyle region is larger, and the animal is smaller. As these traits show considerable intraspecific variation in other *Candelabrum* species, they are here also considered as such.

Candelabrum verrucosum is easily distinguished from *C. phrygium* by the nematocyst buttons on the sporosacs, but it differs additionally by being monoecious. Otherwise, both species are very similar. Only two blastostyles could be used to make serial histological sections. Both blastostyles had female sporosacs of all develop-

mental stages (some containing almost fully formed young polyps) and a single male sporosac filled with spermatids. The male sporosacs are smaller than the female ones.

Genus *Monocoryne* Broch, 1910

TYPE SPECIES: *Coryne gigantea* Bonnevie, 1898b.

SYNONYMS: *Symplectanea* Fraser, 1941 (see Rees, 1958).

DIAGNOSIS: Hydroid solitary or a few polyps in loose aggregates that may have a common perisarc base. Hydranth long, cylindrical, divided into tentaculate body and foot region. Foot covered by thin perisarc, with root-like attachment processes. Hydranth body with scattered capitate tentacles, at least some of them compound tentacles, i.e. branched tentacles with a common epidermis at the base, bases of the side-branches adnate to the side of the main tentacle for some distance, all ends capitate. Gonophores fixed sporosacs developing directly on hydranth body, associated or not with tentacles.

REMARKS: For more details consult Rees (1956, 1958), Petersen (1990), or Stepanjants *et al.* (2003). The European fauna comprises one species only. Stepanjants *et al.* (2003) give an overview on all species.

Monocoryne gigantea (Bonnevie, 1898)

Fig. 10

Coryne gigantea Bonnevie, 1898b: 4, pl. 1 fig. 1.

Monocoryne gigantea – Broch, 1910: 138; Broch, 1916: 12, pl. 1 fig. 1; Johannesen, 1924: 1, figs 1-7, pl. 1-2; Rees, 1956: 117, figs 1-2; Rees, 1957: 488, fig. 38; Calder, 1972: 222, pl. 1 fig. 4; Antsulevich, 1988: 931, fig'd; Petersen, 1990: 203; Stepanjants *et al.*, 2003: 100, figs 1A-F, 6.1.

DIAGNOSIS: *Monocoryne* species up to 15 mm; compound tentacles with two to four capitate ends, usually three; hermaphroditic, sporosacs in upper axils of compound tentacles.

DESCRIPTION: (after Bonnevie, 1898b; Johannesen, 1924; Rees, 1956; Stepanjants *et al.*, 2003) Vermiform hydranths, solitary or clustered into loosely joined aggregates, attached laterally to substratum by curved proximal end; divisible into foot (caulus) zone and tentaculate part. Foot roughly 1/2 of total length, covered by close fitting, soft, thin perisarc, in lower half of foot several large, distinct anchoring filaments with widened distal end. Tentaculate part also about 1/2 of length, but very extensible and active in life, all tentacles distinctly capitate with spherical capitula, very extensible, around mouth about eight simple capitate tentacles, below them many (< 30) scattered compound tentacles and also some simple ones. Compound tentacles usually with three, sometimes two or four capitate ends, with middle branch(es) thickest and longest, the side-branches originate near its base and are adnate for some distance before they become free, the fused part forming a plate-like base with a common epidermis. Gonophores sessile sporosacs arising in the upper axils of the compound tentacles, sporosacs oblong, without radial canals; male, female and hermaphroditic sporosacs can be produced by the same animal (Broch, 1916; Johannesen, 1924). Nematocysts: stenoteles, microbasic mastigophores, desmonemes, microbasic euryteles.

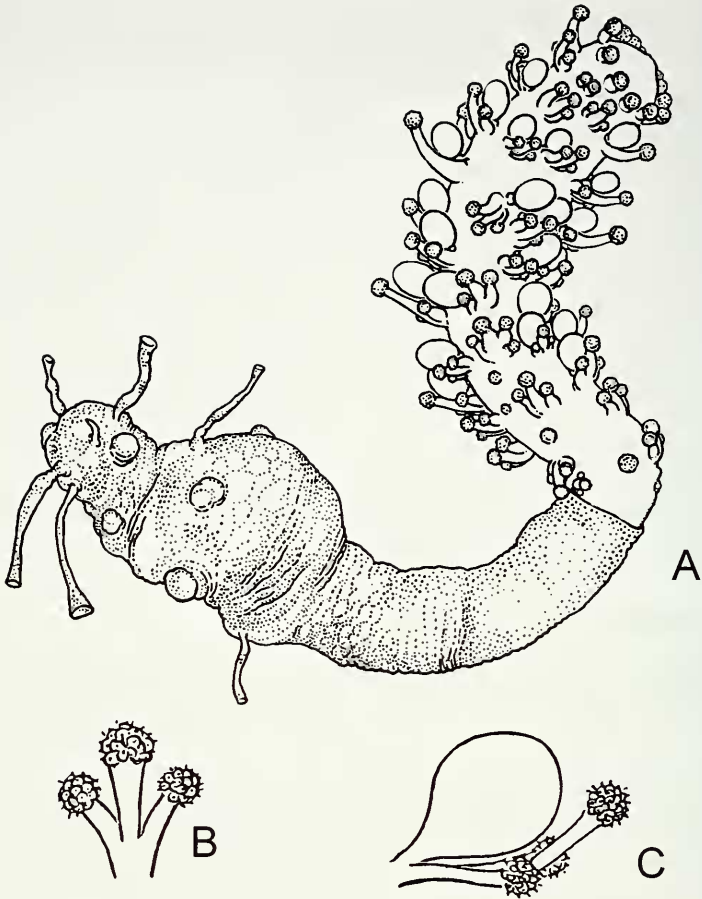


FIG. 10

Monocoryne gigantea (Bonnievie, 1898), modified from Rees (1956). A) Whole polyp, foot with perisarc stippled dark. B) Compound tentacle. C) Side view of sporosac in axil of compound tentacle.

DIMENSIONS (Rees, 1956; Stepanjants *et al.*, 2003; consult these references for additional measurements): Fertile polyps 11-15 mm (preserved material), diameter of hydranth body 1.4-1.7 mm, length of gonophores 0.6-0.9 mm, diameter 0.4-0.5 mm. Nematocysts: stenoteles (14-18) \times (12-18) μ m; microbasic mastigophores (19-24) \times (8-11) μ m; desmonemes 10 \times 8 μ m, microbasic euryteles (22.5-25) \times (12-12.5) μ m.

BIOLOGY: A rare species, occurs usually in waters of 100 m depth and more, but in the high Arctic archipelago Franz Joseph Land it was found in only 16-20 m (Antsulevich, 1988). Known substrata (Swenander, 1904) are a *Tubularia* spec. and polychaete tubes, both attached on shells of the bivalve *Lima excavata*.

DISTRIBUTION: Arctic species, with its southern limit in the Trondheimsfjord (Johannesen, 1924). It has been recorded from northern Norway (Bonnievie, 1898b),

Franz Joseph Land (Antsulevich, 1988), North-Eastern Canada (Calder, 1972). Type locality: Hammerfest, Norway.

REMARKS: Rees (1958) synonymized the genera *Symplectanea* and *Monocoryne*, but kept *M. bracteata* provisionally distinct from *M. gigantea* because of its larger size and the greater number of capitate heads per compound tentacles, but he suggested that more material might show it to be synonymous with *M. gigantea*. It could be that *Monocoryne bracteata* is dioecious, thus differing from the monoecious *M. gigantea*. The only other named species of the genus is *Monocoryne minor* Millard, 1966. It is smaller and its sporosacs develop independently of the tentacles.

FAMILY TRICYCLUSIDAE KRAMP, 1949

DIAGNOSIS: Solitary, usually benthic hydroids, having a conical to pear-shaped hydranth and tapering pedicel ending in a small attachment disc. Pedicel covered in a loose, filmy or gelatinous perisarc. Tentacles in three whorls, one oral whorl, one in middle of hydranth body, and one near base of body. Oral tentacles capitate, other tentacles also capitate but bearing additional nematocyst clusters. Vegetative budding of hydranths below proximal tentacles. Gonophores develop above proximal set of tentacles and remain fixed. Male gonophores medusoid, with radial canals and circular canal. Female ones without canal system. Cnidome: Stenoteles, desmonemes, and heteronemes.

Genus *Tricyclusa* Stechow, 1919

TYPE SPECIES: *Tiarella singularis* Schulze, 1876.

SYNONYM: *Tiarella* Schulze, 1876.

DIAGNOSIS: As for the family.

REMARKS: The genus *Tricyclusa* is currently monotypic, containing only *Tricyclusa singularis* (Schulze, 1876). Schulze (1876) originally proposed the genus name *Tiarella* for this species. Because this name is preoccupied for a gastropod and also other taxa, Stechow (1919: 6) proposed the new name *Tricyclusa*. It is a characteristic genus and it poses no taxonomic problems.

Tricyclusa singularis (Schulze, 1876)

Fig. 11

Tiarella singularis Schulze, 1876: 415, pls 29-30; Bedot, 1911: 209, pl. 11 fig. 2.

Tricyclusa singularis – Stechow, 1919: 6; Rees, 1941: 133, fig. 3; Rees, 1957: 462, 505, figs 6 & 51B; Picard, 1957: 10; Vevers, 1959: 506, figs 1-6; Teissier, 1965: 10; Bouillon, 1974: 142; Petersen, 1990: 146, fig. 15; Bouillon *et al.*, 2004: 103, fig. 55D.

Margelopsis stylostoma Hartlaub, 1903: 28, fig. 2; Hartlaub, 1907: 91, fig. 87; Bedot, 1911: 211; Rees, 1941: 133.

MATERIAL EXAMINED: BMNH 1957.6.26.1-10, Roscoff intertidal, leg. Cantacuzène, on red algae, numerous well preserved specimens. – BMNH 1956.11.7.7-13, Baie de Morlaix, 23 June 1955, coll. W.J. Rees, on *Chorda filum*, several contracted specimens.

DIAGNOSIS: As for the family.

DESCRIPTION (after literature and observed material): Hydroid solitary, usually attached to algae, sometimes freely floating, divided into hydranth body and pedicel,

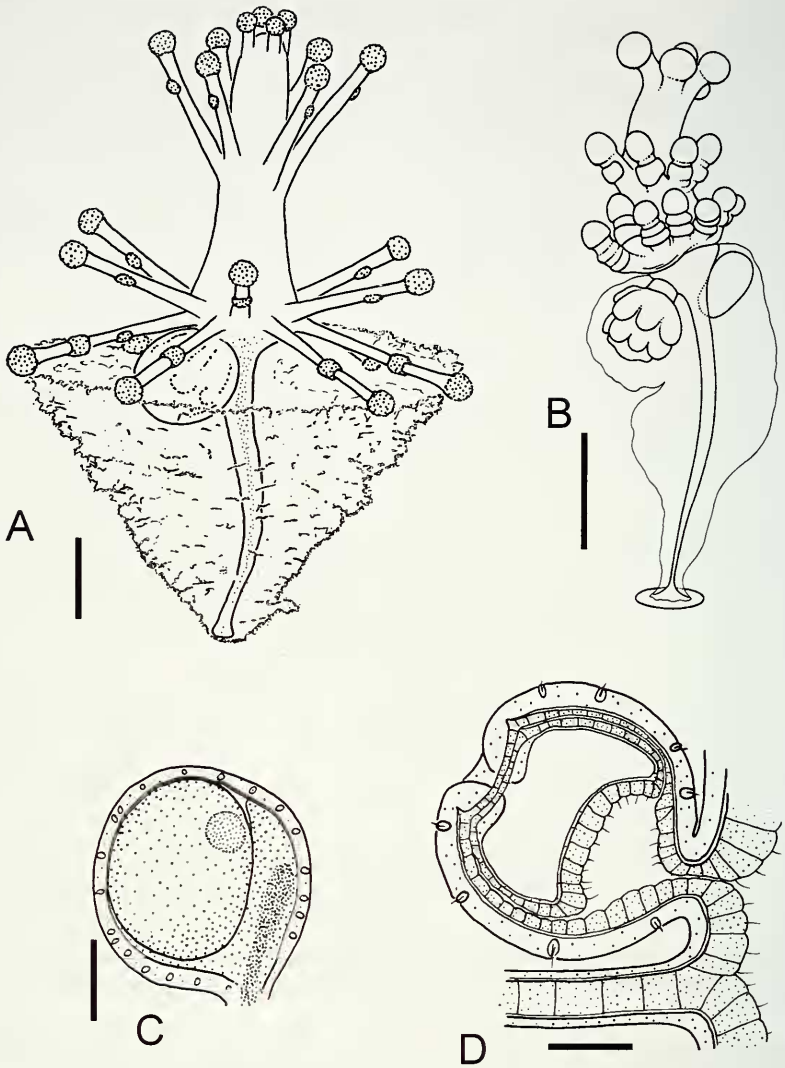


FIG. 11

Tricyclusa singularis (Schulze, 1876), after preserved material. A) BMNH 1957.6.26.1-10, Roscoff, polyp with long tentacles, scale bar 0.2 mm. B) polyp with short tentacles, after Petersen (1990), scale bar 0.5 mm. C) Optical section of a female sporosac, modified after Bedot (1911), scale bar 0.2 mm. D) Optical section of a male medusoid after it has liberated its gametes, modified after Schulze (1876), scale bar 0.05 mm

both of about the same length. Pedicel in a conical, loose, filmy or gelatinous periderm cup, wrinkled, with adhering detritus particles. Pedicel tapering proximally, ending at base in a small attachment disc. Hydranth pear-shaped to conical, broadest near lower end, with three distinctly separated sets of tentacles, tentacle gastrodermis chordoid. Oral tentacles in one whorl, four to five in number, short, capitate, directed upwards;

middle whorl of tentacles approximately in middle of body, usually six in number, directed obliquely upwards, with terminal nematocyst knob and with or without additional one to two knobs in distal half of tentacle; basal tentacles 10 to 14, usually 12, in two closely approximated whorls, alternately pointing up- and downwards, with terminal knob and additionally one or more proximal knobs, these either clasping or encircling tentacle. Underneath lowest tentacles vegetative polyp buds, one to six in number, budded polyps are released as small, fully formed hydranths but have a short pedicel, newly released polyps may already have incipient gonophores. Gonophores develop immediately above basal whorl of tentacles, spherical, remaining attached to hydroid. Male gonophores with four radial canals and ring canal, thus of medusoid type. Female gonophores sporosacs without canal system, with one large egg. Nematocysts: Stenoteles, desmonemes, microbasic euryteles.

DIMENSIONS: Total height around 2 mm, hydranth about 1 mm high, hydranth base diameter 0.4-0.6 mm. Female sporosacs after Bedot (1911) about 0.6 mm, male medusoids after Schulze (1876) about 0.2 mm.

ADDITIONAL DATA: The length of the tentacles is variable, and this is not only due to contraction. Young individuals and polyps found in the plankton have very long and thin tentacles that get shorter once the animal attaches itself (Bedot, 1911). Young animals and those from the plankton also have a short pedicel.

DISTRIBUTION: Adriatic Sea, Northern Brittany, western Ireland. Type locality: Adriatic Sea, Trieste, Bay of Muggia (Italy), on *Cystoseira*.

BIOLOGY: The polyps live attached to various macroalgae and *Zostera* plants near the low-water-mark (Rees, 1941, Teissier; 1965). Occasionally, detached polyps can be found in the plankton, but this is not the usual mode of life (Bedot, 1911). In Brittany it occurs mainly from May to July, although some animals were also found during March and April (Bedot, 1911; Teissier, 1965). In the Mediterranean it was found in April (Schulze, 1876). The fertile period for Brittany is from May to June (Bedot, 1911; Teissier, 1965). It is a rare species, but when present, it can occur in large numbers (Bedot, 1911).

REMARKS: *Tricyclusa singularis* (Schulze, 1876) is a characteristic and unproblematic species. Hartlaub (1903, 1907) described a similar species from the plankton of Roscoff which he named *Margelopsis stylostoma*, differing mainly only in the short pedicel. Even Hartlaub (1903, 1907) suspected that it was only a planktonic form of *Tricyclusa singularis*. It was later synonymized with *Tricyclusa singularis* by Bedot (1911) and Rees (1941).

Although easy to identify and despite its presence near the water surface, this animal has only rarely been reported. After its discovery, it has never been found again in the Mediterranean Sea. It seems that it is only occasionally present and quite seasonal. Most regularly it has been seen at Roscoff (Brittany). It is particularly interesting to note that it has never been reported from the other side of the English Channel, despite England being one of the best investigated regions. Perhaps it prefers warmer waters, an assumption also underlined by its occurrence during the summer months. Probably it survives unfavourable conditions through a sexually produced resting stage.

FAMILY MARGELOPSIDAE UCHIDA, 1927

TYPE GENUS: *Margelopsis* Hartlaub, 1897.SYNONYM: *Pelagohyridae* Dendy, 1902.

DIAGNOSIS: Hydroid solitary, pelagic; hydrocaulus absent or reduced to a small process; hydranth body vasiform, tentacles filiform to moniliform, arranged into two separate sets, oral tentacles in one or several whorls; aboral tentacles either in two to three alternating whorls or numerous and scattered over most of body. Gonophores free medusae, medusa buds develop among tentacles or above aboral tentacles.

Medusa manubrium with simple mouth; gonads surrounding manubrium entirely; four radial canals; tentacles solid, generally moniliform, two or more tentacles per marginal bulb, in some genera tentacles also issuing at different levels on exumbrella; without ocelli.

REMARKS: With its clustered marginal tentacles in the medusae and the pelagic polyps, this is a distinct and characteristic family of the Capitata. It comprises the genera *Climacocodon* Uchida, 1924, *Margelopsis* Hartlaub, 1897, and *Pelagohydra* Dendy, 1902 (Petersen, 1990). The well established and frequently used name Margelopsidae Uchida, 1927 is threatened by the senior synonym Pelagohyridae Dendy, 1902. The latter name has not been used and for the sake of nomenclatural stability it is preferable to continue to use Margelopsidae. According to the ICZN [article 29.3.1.1] there is no need to change it to the formally correct Margelopsididae.

KEY TO GENERA:

- 1a medusa with several tentacle pairs on exumbrella
 *Climacocodon* (not in European fauna)
 1b medusa tentacles in four groups along bell margin: 2
 2a polyp with caulus rudiment, aboral tentacles in two to three close whorls . . *Margelopsis*
 2b polyp without caulus rudiment, aboral tentacles scattered
 *Pelagohydra* (not in European fauna)

***Margelopsis* Hartlaub, 1897**TYPE SPECIES: *Margelopsis haeckelii* Hartlaub, 1897 by monotypy.

DIAGNOSIS: Hydroid with hydrocaulus rudiment, without parenchymatic specializations of the gastrodermis; tentacles indistinctly moniliform; oral tentacles in one whorl, aboral ones in two to three whorls, medusae buds above aboral tentacles.

Medusa with four perradial tentacular bulbs on bell margin, each with two to six solid tentacles.

REMARKS: There are two species of *Margelopsis* in the European fauna, namely *Margelopsis haeckelii* and *M. hartlaubii*. See the diagnoses for ways to distinguish them.

***Margelopsis haeckelii* Hartlaub, 1897**

Figs 12-13

Margelopsis Haeckelii Hartlaub, 1897: 482, pl. 16b figs 12-18; Hartlaub, 1899: 219, figs 1-3 [hydroid].

Margelopsis haeckeli – Hartlaub, 1907: 89, 91, figs 84-86; Müller, 1908: 43, pl. 4 figs 12-17, pl. 5 figs 18-19; Mayer, 1910: 80, fig. 38; Leloup, 1930: 97, fig.; Kramp, 1930: 12; Kramp, 1937: 32, fig. 10; Thiel, 1938: 294; Leloup, 1946: 1; Russell, 1953: 95, figs. 41A-C,

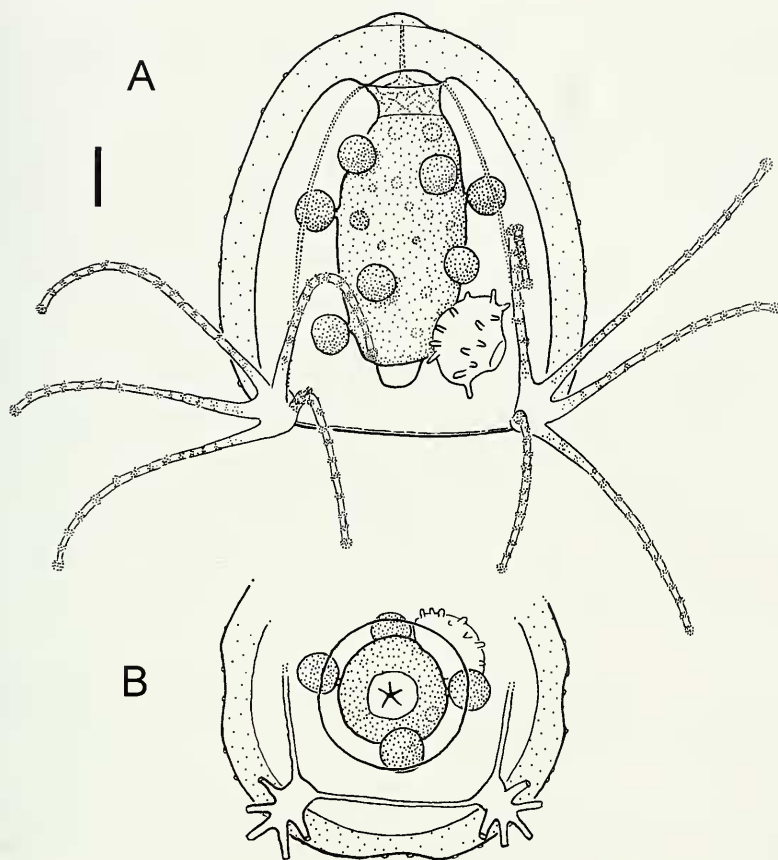


FIG. 12

Margelopsis haeckelii Hartlaub, 1897; schematic pictures derived from various preserved samples. Mature medusa with subitaneous eggs and one young polyp, scale bar 0.3 mm. B) Oral view of a medusa, tentacles clipped, same scale as A.

42A-B; Werner, 1954: 124, figs 1-9; Werner, 1955: 1-30, figs 1-9; Prévot, 1959: 104, pl. 3 fig. 11; Kramp, 1959: 92, fig. 47; Kramp, 1961: 49; Russell, 1970: 234; Bouillon, 1974: 143.

MATERIAL EXAMINED: BMNH 1967.5.25.1-8, Helgoland, 12 May to 24 July 1958, medusae and polyps. – BMNH 1967.5.25.6, 2 medusae from Sylt, 10 July 1958, with resting eggs. – Zoological Museum Hamburg, about 50 mature medusae, collected in plankton by B. Werner, 24 July 1958, with subitaneous and resting eggs. – Zoological Museum Hamburg, several polyps from List, collected 27 June 1961, cultivated by B. Werner, with medusae buds.

DIAGNOSIS: *Margelopsis* polyp with vasiform body, stalk rudiment, two well-separated sets of tentacles, medusae buds in one whorl oralward of aboral tentacles. Medusae of up to 2 mm high, umbrella bell-shaped, moderately thick, apical canal present, 3-6 tentacles per bulb, manubrium base with large vacuolated cells, usually only females present, eggs of two types: subitaneous eggs developing directly into polyp stage, diapausing eggs developing first into encysted resting stage.

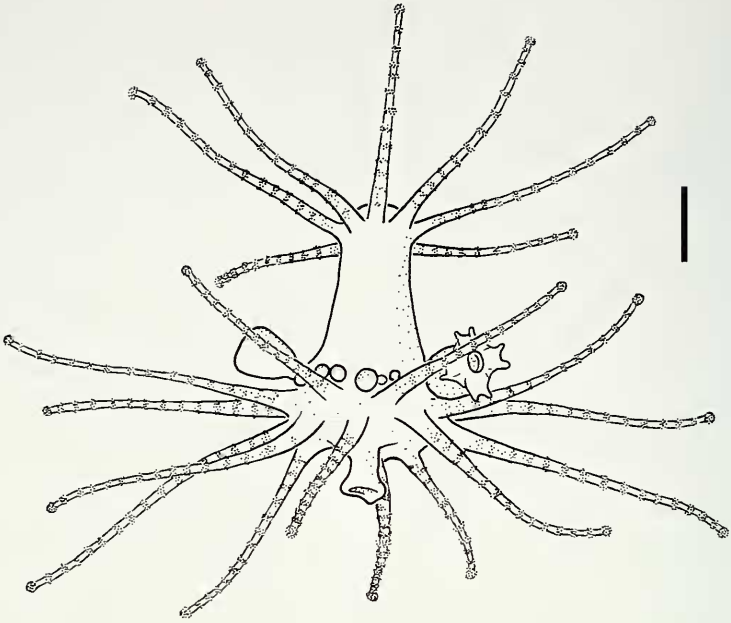


FIG. 13

Margelopsis haeckelii Hartlaub, 1897; schematic picture derived from various preserved samples. Polyp with medusae buds, oral side above. scale bar 0.2 mm.

DESCRIPTION (after examined material and literature): Newly released polyps actinula-like, ovoid, with short tentacles, tentacles numbers slightly lower than in fully mature animals.

Mature polyp planktonic, body vase-shaped, resembling a detached tubularian hydranth, at aboral end a short stalk rudiment with a central depression. Tentacles in two well-separated sets, rather stiff, with nematocysts concentrated in rings and a small terminal knob, base of tentacles free of nematocysts. Aboral tentacles slightly longer than oral ones, 12-15 in two closely approximated whorls, alternately pointing obliquely up- and downward. Oral tentacles around short conical hypostome, five to eight in number. Medusae buds borne on body of hydranth just oralward of the aboral tentacles, sometimes groups of medusa buds on a short stalk. Medusae develop without envelope, the tentacles are free and not tucked into the subumbrella as in most other hydromedusae.

Umbrella of very young medusae relatively wider than in adult, apical jelly thin, nematocysts evenly scattered over exumbrella; broad umbilical canal, stomach length less than half the height of subumbrellar cavity, a circle of nematocysts surrounds the mouth-opening, without gonads. Four radial canals and ring-canal narrow. Four perradial marginal bulbs each with two to three tentacles. Tentacles covered with scattered clusters of nematocysts, but base of tentacles without nematocysts. Umbilical canal and marginal bulbs with black pigment. Umbrella becomes higher with further

growth. In a specimen 1.5 mm high, apical jelly considerably thicker than sides of umbrella, many exumbrellar nematocysts, umbilical canal has narrowed, stomach considerably longer. Upper third of stomach without gonads, with large gastrodermal cells covered by thin layer of epidermis. Gonad covering lower two-thirds of the stomach thin. Three to four tentacles irregularly placed on each marginal bulb, with irregularly scattered nematocysts which appear as ring-like bands when tentacle contracted. Upper basal third of stomach clear and transparent in contrast to opaque brownish grey appearance of lower part.

Adult medusa with bell-shaped umbrella, slightly higher than wide, without apical process or with small apical process; with scattered exumbrellar nematocysts; jelly moderately thick, thicker at apex, velum moderately broad to narrow. Stomach cylindrical, length $\frac{2}{3}$ to $\frac{1}{1}$ of subumbrellar height; basal portion with large transparent gastrodermal cells; apical canal regularly present (rest of umbilical canal); mouth simple, circular, margin armed with nematocysts. Four radial canals and ring canal narrow. Gonad surrounding stomach, leaving upper third free. Eggs amoeboid, embryos developing attached to manubrium on pedicel, depending on season either into young polyp or encysted resting stage. Four periradial rounded marginal bulbs, each with four to seven somewhat stiff tentacles, usually irregularly radiating, with nematocysts concentrated in rings and a small terminal knob, thus nearly moniliform, gastrodermal cells chordoid. No ocelli. Colour of stomach dark grey with dark brown pigment granules; marginal bulbs brown. Nematocysts desmonemes, basitrichous haplonemes, microbasic euryteles, stenoteles.

DIMENSIONS: Adult medusa up to 2 mm high, subitaneous egg production starts at a bell diameter of 1-1.5 mm and with 3-5 tentacles per bulb, resting eggs are produced by full sized animals only; subitaneous eggs 0.12-0.13 mm, resting eggs 0.18-0.21 mm; newly released medusa 0.5 mm; newly released polyp resulting from subitaneous eggs 0.3-0.4 mm, adult polyps 1-2 mm (Werner, 1954), aboral tentacles as long as hydranth or slightly longer.

BIOLOGY: Polyps and medusae are usually present in the plankton from June to September, but they have also been seen earlier. They are thought to remain floating through water currents, as they sink in still water. Their numbers fluctuate drastically from year to year. Werner (1954, 1955) made detailed investigations on the life history and development of this species. Male medusae appear to be extremely rare; Werner (1954) observed only one hermaphrodite in 250 medusae, the others being all female. The immature eggs are amoeboid and grow by engulfing other eggs (Müller, 1908). The eggs develop parthenogenetically (Werner, 1956). Two different types of eggs are produced: smaller subitaneous eggs and larger resting eggs. Both egg types start their development attached to the manubrium by a small stalk. The total production of subitaneous eggs depends on the food availability of the medusa and varies in number from a few eggs to 30 or 40. For the most part, only two to three egg cells mature and emerge at the same time. Often a medusa bears 20-30 eggs and embryos on the manubrium, of different ages and different developmental stages. The subitaneous eggs are produced earlier when water temperatures are between 7 and 15°C. They develop directly within four to ten days into a small polyp that is then released from the medusa. Later in the

year, when water temperatures exceed 15°C, the production of subitaneous eggs stops and resting eggs are produced. These are larger than the subitaneous eggs and possess nematocysts on their surface. Generally, only one or two of this type are formed at the same time and usually not more than six of them remain attached to the manubrium. The initial development takes place when the egg is attached to the manubrium and reaches a 'stereo-blastula' stage (a thin layer of ectodermal cells surrounds a mass of yolky endodermal cells). At this stage development stops, the egg detaches and sinks to the bottom, where it may attach or not as a lens-shaped cyst. The nematocyst layer helps in the attachment process. The embryo forms a periderm capsule with a characteristic polygonal pattern. The animal overwinters then as a cyst and after 6-9 months a small polyp hatches in the next spring (Werner, 1984). The newly released polyp lives in the plankton where it grows to full size and then produces medusae.

It seems that only few resting stages survive the winter, as initially there are only very few hydroids in the plankton. However, through the following medusa production and the polyps resulting from their subitaneous eggs, the population density can grow very rapidly (Werner, 1955).

DISTRIBUTION: Southern North Sea and Irish Sea. Helgoland (Hartlaub, 1897; 1899; Werner, 1955); Norfolk coast (Hamond, 1964), Solway Firth (Russell, 1970), Weser, Elbe, and Ems Estuary (Kühl, 1962, 1967; 1971), Belgium (Kramp, 1930; Leloup, 1947). Type locality: Helgoland.

ADDITIONAL DATA: The medusae swim very energetically and jerkily. The short marginal tentacles are held out rather stiffly (Hartlaub, 1907).

Hartlaub (1907) observed that the polyps normally do not swim actively and sink slowly to the bottom of the vessel. When sinking, the aboral pole is on top. The polyps are very sensitive to temperature fluctuations. These observations could not entirely be confirmed by Werner (1955), who observed that the polyps do not regularly sink with the oral pole downward, and he thinks that the polyp in the free water does not necessarily orient itself with the aboral pole uppermost.

The aboral stalk rudiment of the polyp has a depression lined with a high epithelium with cylindrical cells, which Hartlaub (1899) considered reminiscent of the pneumatophore of the Physophorae. *Margelopsis haeckelii* has been seen as a model representing an intermediate stage in the evolution of the Siphonophorae (Totton, 1965). This view was contested by Werner (1955), who observed that this organ is used by the hydroid to attach itself temporarily, acting like a sucker organ. The cells of the depression secrete a mucus that is often infested with detritus particles. The aboral stalk rudiment is thus clearly homologous to the corresponding organ by which the tubularian actinula larva attaches itself, and ultimately also the stalk of the mature hydranth.

When the medusa switches from the production of subitaneous- to resting eggs, there may be a period when there are no conspicuous eggs on the manubrium. Such medusae can easily be mistaken for mature males, although they do not have any spermatids (Werner, 1955).

Prévot (1959) depicts a longitudinal section of the polyp. The stalk carrying the medusae buds (blastostyle) is hollow and communicates with the stomach. In the polyp material examined for this study, one bifid oral tentacle was seen.

REMARKS: The original spelling in Hartlaub (1897) is *Margelopsis haeckelii*, which must be retained, despite that Hartlaub (1907) used *haeckeli*, a spelling then used by all subsequent authors (the specific epithet *haeckelii* is the genitive form of the latinized name Haeckelius).

In his study on medusae of Charleston Harbor, McCrady (1859) also described *Nemopsis gibbesii*. His description was mainly based on a series of medusae that are clearly referable to the genus *Nemopsis* (Bougainvilliidae). But McCrady also found a polyp in the plankton which he erroneously associated with this medusa. The polyp closely resembles the polyp of *Margelopsis haeckelii*, only differing in the medusae buds that are dispersed between the two whorls of tentacles. McCrady (1859: figs 4-6) also describes and depicts young medusae stages released by this polyp. As A. Agassiz (1862) and Hartlaub (1899) have already pointed out, McCrady's medusae from the plankton (McCrady, 1859: figs 1-3) were actually *Nemopsis bachei* L. Agassiz, 1849. Therefore, Hartlaub (1899) restricted the name *Margelopsis gibbesii* to the polyp described by McCrady. Although the first revisor was A. Agassiz (1862) who synonymized the name *N. gibbesii* with *N. bachei*, Hartlaub's proposal was followed by Mayer (1910) when he attributed some *Margelopsis* medusae from North Carolina to *M. gibbesii*. McCrady's description did not include mature medusae and the allocation of Mayer appears unfounded, but there is a reasonably good chance that Mayer's identifications were correct, as there are no other *Margelopsis* medusae known from the region.

Thiel (1938) found a *Margelopsis* medusa in the Southern Ocean, which he assigned to *M. gibbesii* and he claimed that *M. gibbesii*, *M. haeckelii* and *M. hartlaubii* are conspecific, a possibility already suggested by Mayer (1910: 80). However, this has not gained acceptance and Kramp (1959) distinguished the medusae of *Margelopsis gibbesii* from *M. haeckelii* by the presence of an apical canal, the thicker jelly and the viviparity in the latter species. The scattered medusae buds in the polyp of *M. gibbesii* can also be added. According to Mayer (1910), *Margelopsis gibbesii* produces male medusae, which indicates that both species differ perhaps also significantly in their life-histories. However, as Werner (1955) cautioned, female medusae that switch from the production of subitaneous- to resting eggs can easily be mistaken for males. More biological details on *M. gibbesii* must be known before both species can be compared and meanwhile it seems appropriate to keep *M. gibbesii* separate from *M. haeckelii*.

Besides *M. haeckelii*, there is also another *Margelopsis* species occurring in the European fauna, namely *M. hartlaubii*. The latter species is known only from the medusa phase occurring in deep waters of Norway, thus contrasting with *M. haeckelii* which is a shallow water species. *Margelopsis hartlaubii* can be distinguished by its lower tentacle number (2-3 per bulb placed beside each other), the thicker jelly, the absence of an apical canal, and the brick-red manubrium.

Margelopsis hartlaubii Browne, 1903

Fig. 14

Margelopsis hartlaubii Browne, 1903: 10, pl. 1 fig. 2, pl. 3 fig. 3; Mayer, 1910: 82, fig. 40; Kramp & Damas, 1925: 252, fig. 4; Kramp, 1959: 91, fig. 49; Kramp 1961: 50.

MATERIAL EXAMINED: Zoological Museum Bergen, No 36451, 15 July 1925, Haggernes, Herdlafjord, 200-400 m, 2 medusae, damaged before fixation. – Zoological Museum Bergen, No

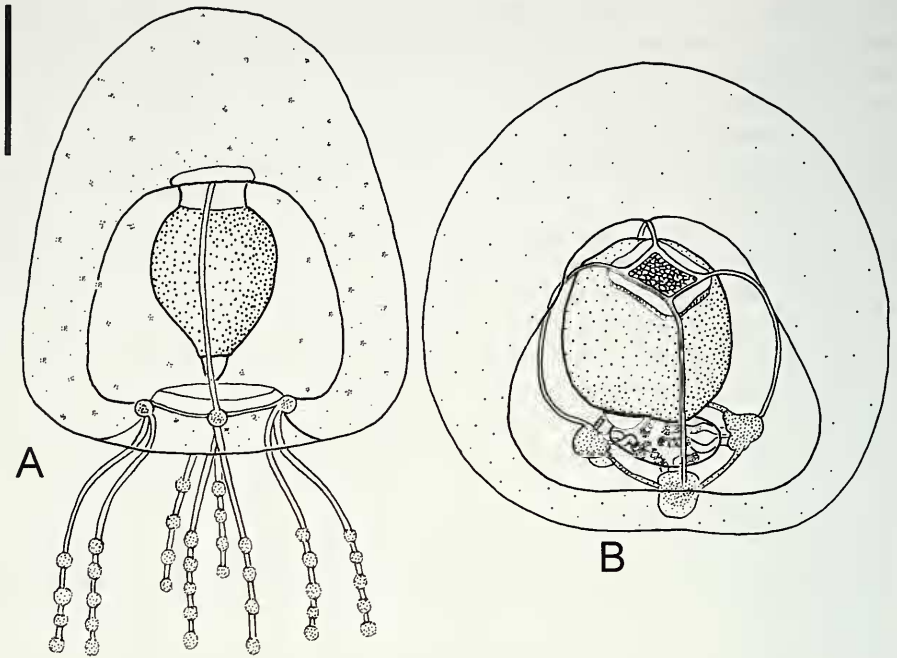


FIG. 14

Margelopsis hartlaubii Browne, 1903. A) Redrawn from Browne, scale bar 1 mm (1903). B) Modified after Kramp & Damas (1925).

26825, Herlöfjord, September 1908 (sic), 1 medusa, fertile female, depicted in by Kramp & Damas (1925). – Zoological Museum Bergen, No 26826, ca. 300 m, September 1908, 2 medusae in bad condition, identified by Kramp & Damas (1925).

DIAGNOSIS: *Margelopsis* medusa measuring 2-4 mm, umbrella spherical to bell-shaped, jelly relatively thick, no apical canal, with two to three moniliform tentacles per bulb, gonads much bulging, likely no brooding of eggs.

DESCRIPTION (after Kramp & Damas, 1925): Polyp stage unknown. Medusa umbrella spherical, 3-4 mm for mature animals, exumbrella with scattered nematocysts. Mesogloea thick, especially at apex, its consistency very soft. The voluminous manubrium takes up a large part of the subumbrellar cavity, its base quadrangular and not covered by gonad; gonad occupies the middle region, shaped like a cube or barrel; oral portion of manubrium conical to cylindrical and mouth margin provided with ring of nematocysts. Four radial canals are narrow and transparent. Four tentacular bulbs thick, triangular, without ocelli, with two or three tentacles with a nematocyst-free base, while the distal region is beaded and end with a terminal knob. Velum broad. Mesogloea and the radial canals perfectly transparent and uncoloured. Stomach, marginal bulbs, and tentacular nematocyst clusters contain a brick-red pigment (observed in living animals).

OWN OBSERVATIONS: Basal, gonad-free region of the manubrium very short; large vacuolated cells could not be seen in the examined preserved material; top of the manubrium is flat, apical canal thus absent; gonad covers most of the manubrium and leaves only short regions uncovered at both ends. Gonad encircles the manubrium without interruption. Tentacle bulbs prominent, their epidermal portion bulging, a gastrodermal chamber present. One sample (26825) mature or almost mature female, numerous eggs are clearly visible within gonad, but no eggs or embryos attached to manubrium as in *M. haeckelii*. Some mature medusae could be mature males. Tentacles distinctly moniliform, apparently quite short, usually two per bulb. Tentacles contain only desmonemes and microbasic mastigophores, stenoteles not observed; small stenoteles seem to be present around mouth opening. Undischarged desmonemes (ca. 15x 10 µm) have a thread with characteristic rope structure. Mastigophores have a spherical capsule of about 10 µm diameter.

BIOLOGY: Occurs in 200-400 m depth, recorded from April to September, but only few records are available.

DISTRIBUTION: Norwegian fjords. No type locality was specified, the original material came from Osterfjord and Herløfjord, 0-400 m.

REMARKS: *Margelopsis hartlaubii* Browne, 1903 is a very rare medusa, known only from a few specimens. Its polyp stage is unknown. The species has been synonymized with *Margelopsis gibbesii* and *M. hartlaubii* by Thiel (1938), a proposal that has not gained acceptance (see remarks under *M. haeckelii*). It is actually quite distinct from *M. haeckelii*: about two times larger, it has a thick mesogloea, it has only two to three tentacles per bulb, and there is no apical canal. Furthermore, the available material suggests that there is no brooding in this species and males may exist.

Nevertheless, more data on this species are needed, e.g. detailed nematocyst data and information on its polyp stage should be obtained in order to confirm the taxonomic position of this species.

FAMILY PENNARIIDAE MCCRADY, 1859

SYNONYM: Halocordylidae Stechow, 1921.

DIAGNOSIS: Hydroid colony pinnate, occasionally bushy, stem monosiphonic, giving rise alternately from opposite sides to two series of hydrocladia; hydrocaulus and hydrocladia with terminal hydranths (monopodial); hydranths on short pedicels on upper side of the hydrocladia; hydranths pear-shaped; tentacles of two types: in distal half of hydranth more or less capitate tentacles in one oral whorl and more in indistinct whorls below, on lower part of hydranth one aboral whorl of semifiliform to slightly capitate aboral tentacles; gonophores developing above aboral tentacles, eumedusoids, liberated or not.

Medusa a simple eumedusoid; manubrium not extending beyond umbrella margin; gonads completely surrounding manubrium; four radial canals; four permanently rudimentary tentacles, usually reduced to mere bulbs, without ocelli.

REMARKS: The family contains only the genus *Pennaria* Goldfuss, 1820.

Genus *Pennaria* Goldfuss, 1820TYPE SPECIES: *Pennaria disticha* Goldfuss, 1820.SYNONYMS: *Globiceps* Ayres, 1854; *Eucoryne* Leidy, 1855; *Halocordyle* Allman, 1872.

DIAGNOSIS: With the characteristics of the family.

REMARKS: There are several medusa-based species (Kramp 1959, 1968). They are mostly indeterminate and some of them do not belong to the genus *Pennaria* at all (Petersen, 1990). For the synonymy and validity of the name *Pennaria* see Calder (1988) and Gibbons & Ryland (1989). Only *Pennaria disticha* is relevant for the European fauna.

Pennaria disticha Goldfuss, 1820

Fig. 15

Pennaria disticha Goldfuss, 1820: 89; Mayer, 1910: 24, fig. 1A-E; Brinckmann-Voss, 1970: 40, text-figs 43, 45-50; Gibbons & Ryland, 1989: 387, fig. 5 [taxonomy]; Schuchert, 1996: 142, fig. 85a-c; Watson, 1999: 16, fig. 10A-I; Bouillon *et al.*, 2004: 103, fig. 55A-C.

Pennaria Cavolinii Ehrenberg, 1834: 297; Allman, 1872: 364, fig. 80.

Pennaria cavolini – Weismann, 1883: 121, pl. 17 figs 1-5, pl. 18.

Halocordyle disticha – Rees & Thursfield, 1965: 4; Millard, 1975: 41, figs 16C-G; Hirohito, 1977: 2, fig. 1, pls 1-3; Garcia-Corrales & Aguirre, 1985: 85, figs 1-3 [synonymy]; Morri & Boero, 1986: 31, fig. 11; Wedler & Larson, 1986: 73, fig. 4C; Calder, 1988: 57, figs 43-45 [complete synonymy]; Hirohito, 1988: 28, figs 9a-d, pl. 1 fig. C; Östman *et al.*, 1991: 607, figs 1-18; da Silveira & Migotto, 1991: 437, fig. 1.

MATERIAL EXAMINED: MHNG INVE29809, Mallorca, Cala Murada, coll. P. Schuchert 24 August, 2000 fertile, depth 1 m, 16S sequence AM088481, 18S sequence AY920762. – MHNG INVE 36918, Naples, coll. 1892, few hydranths left. – MHNG INVE 36919, Naples, coll. 1900, fertile. – MHNG INVE 36920, origin unknown, likely Mediterranean, fertile. – MHNG INVE 35468, USA, North Carolina, Morehead City, marine anchorage, fertile, collected 7 October 2000 by Dr Alberto Lindner. – BMNH 1964.8.7.5 *Pennaria tiarella*, slide preparation, Woods Hole, Mass. USA, fertile, hydrocladia bearing a single hydranth, stenoteles max. 25 μ m, thus larger than in Weill (1934) and within the range observed for *P. disticha* (Hirohito, 1977). – Honduras, Utila, Blue Bayou Beach, coll. F. Sinniger 13 February 2004, depth 1 m, hydranths more delicate than European forms. – Thailand, Andaman Sea, Koh Phi Phi, Ao Nui, 16 April 2000, 10-20 m, collected by Dr A. Faucci. – New Zealand, Hauraki Gulf, Devonport, 26 July 2002, one medusa from plankton. – See also Schuchert (1996, 2003).

DIAGNOSIS: Feather-like branched hydroid colony (pinnate), firm perisarc, gonophore medusoid, released or not, with four bulbs, no ocelli.

DESCRIPTION: Hydroid colonies forming branching, feather-like shoots, arising from thick creeping, ramified stolons. Growth monopodial with hydranths on all ends. Main axis thick, often curved, monosiphonic, perisarc with smooth stretches and annulated stretches in more or less regular intervals, regularly so distal to insertion of hydrocladia (side-branches) and hydranth pedicels. Hydrocladia of one side form an angle of about 120-140 degrees with those from other side, curved, longest hydrocladia usually found at about 1/3 to 1/2 stem length (measured from base), hydrocladia are about half as thick as stem, they either bear hydranths on pedicels (ramuli) or secondary hydrocladia with hydranths again on pedicels. Pedicels (ramuli) of hydranths originate on upper side of hydrocladia, all approximately of same length and evenly spaced, with annulation at their base or throughout, younger ones without annulation. Hydranths spindle- to pear shaped, hypostome dome-shaped. Tentacles of two types: an aboral whorl of about 12-14 long, filiform to slightly capitate tentacles and

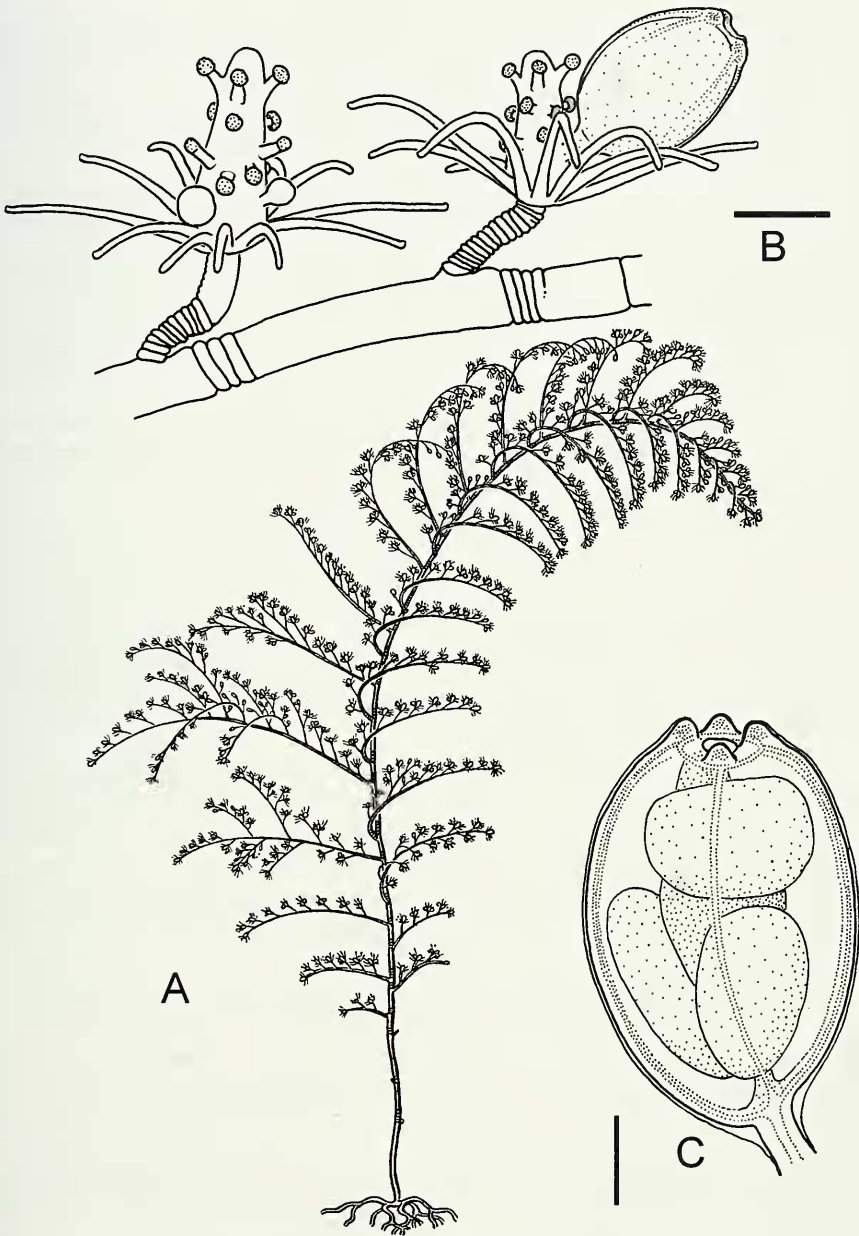


FIG. 15

Pennaria disticha Goldfuss, 1820, after Mediterranean material. A) Colony, modified after Mayer (1910), actual size. B) Part of branch with two hydranths, one with an almost mature medusoid, scale bar 0.5 mm. C) Female medusoid that has already spawned some eggs, modified after García-Corrales & Aguirre (1985), scale bar 0.2 mm.

up to 16 short capitate tentacles distributed in two to three indistinct whorls on distal half of hydranth. Knobs of capitate tentacles, except of oral ones, can be reduced to mere nematocyst cap, thus being almost filiform. Nematocysts of aboral tentacles mainly on aboral side and terminally (= semifiliform according to Petersen, 1990), aboral epidermis of filiform tentacles about three times thicker than on oral side, gastrodermal cells chordoid.

Gonophores oblong medusoids arising on short pedicels just above whorl of long filiform tentacles. Gonads encircling manubrium, four radial canals and circular canal present, with four marginal bulbs, with small velum, without ocelli, tentacles normally absent, rarely some rudiments present. Marginal bulbs without a concentration of nematocysts. Colonies gonochoristic, female medusoids with four to six eggs. Gonophores can be released as short-lived medusoids, or they spawn while still attached to hydroid.

Nematocysts of polyp: stenoteles of three to four size classes, microbasic mastigophores with inclusion body, microbasic heteronemes without inclusion body, basitrichous isorhizas, desmonemes. Medusoids with stenoteles only.

Colour of stem dark brown to black, hydrocladia brown, fading distally to clear.

DIMENSIONS: Fertile colonies usually around 8-15 cm high, but may exceptionally reach 40 cm. Hydranths 0.9-1.5 mm high; medusoids 0.7-1.1 mm. More measurements are given in García-Corrales & Aguirre (1985). Nematocyst sizes can be found in Millard (1975), Hirohito (1977), García-Corrales & Aguirre (1985), Calder (1988), da Siveira & Migotto (1991), Östmann *et al.* (1991), Schuchert (1996), Watson (1999). Some of these authors also figure them.

BIOLOGY: Occurs usually in shallow waters of a few meters depth along rocky coasts with some wave action. In the Mediterranean, the colonies are active from spring to fall, the colonies overwinter as stolons (Brinckmann-Voss, 1970; Morri & Boero, 1986). In more tropical waters they can also be present all year round. Spawning is induced by a reduction of the light intensity (sunset) (Baker, 1936; Brinckmann-Voss, 1970; Calder, 1988; Genzano & Kubota, 2003). The eggs develop in the open water.

Sometimes, the colony form can vary quite drastically, the normal pinnate form can intergrade with a more bushy form (da Silveira & Migotto, 1991). Also Calder (1988) found that the colony form varies depending on wave exposure: colonies from sheltered places were more gracile, internodes of both branches and stem were long and slender, branches and ramuli elongate, while specimens from wave-swept ledges were small and compact, internodes of caulus and branches were thicker and shorter and the branches and ramuli relatively shunted. However, the annulation did not differ significantly.

Prey capture and nematocyst function were investigated by e. g. Clark & Cook (1986); Östman *et al.* (1991), and Kem & Östman (1992). The feeding biology was examined by Pardy *et al.* (1968, as *Pennaria tiarella*).

This species has been the subject of a considerable number of experimental and developmental studies (sometimes under the synonym *Pennaria cavolinii*). Regeneration studies have been made by Cerfontaine (1902), Gast & Godeeski (1903),

Brinckmann-Voss (1970), Tardent (1963, 1965). Hydranth development is described and depicted in Berrill (1952). Gonophore development is documented by Weismann (1883), Berrill (1952), and García-Corrales & Aguirre (1985). Gametogenesis was examined by Weismann (1883). Initially, there are many oogonia in female gonophores, but only a few grow to full size and the others are phagocytosed.

There are many reports on the early development and ultrastructure based on populations from the USA, either named *Halocordyle disticha* or *Pennaria tiarella* (e. g. Hargitt, 1899, 1900, 1904; Cowden 1964, 1965a, 1965b; Summers & Haynes, 1969; Summers, 1970, 1976; Lesh-Laurie, 1976; Thomas *et al.*, 1987; Martin, 1980, 1987, 1988a, 1988b, 1990, 1991, 1992a, 1992b, 2000; Martin & Archer, 1986a, 1986b, 1997; Martin & Thomas, 1977, 1981a, 1981b, 1983; Hotchkiss *et al.*, 1984; Brumwell & Martin, 1996).

DISTRIBUTION: Circumglobal in warm temperate to tropical waters. The occurrence at the Azores (Cornelius, 1992) and the Strait of Gibraltar (Medel & López-González, 1996) seem to mark the northern limit for the eastern Atlantic. In the North-Eastern Atlantic also known from the Cape Verde Islands (Rees & Thursfield, 1965), Madeira (Wirtz & Debelius, 2003). Widespread in the western Mediterranean (e. g. Brinckmann-Voss, 1970; García-Corrales & Aguirre, 1985; Bouillon *et al.*, 2004) and eastern Mediterranean (e. g. Vervoort, 1993). Often recorded from the western Atlantic (e. g. Vervoort, 1968; Hirohito, 1977; Wedler & Larson, 1986; Calder, 1988; Migotto, 1996). The distribution further includes the Red Sea (Hirohito, 1977; Vervoort, 1993), Indian Ocean (e. g. Ritchie, 1910; Jarvis, 1922; Stechow, 1925; Mammen, 1963; Millard & Bouillon, 1973; Millard, 1975; Watson, 1999), Malayan Archipelago (Pictet, 1893; Schuchert, 2003), North-Eastern Pacific (Hargitt, 1927; Hirohito, 1977; 1988); south-western Pacific (Schuchert, 1996; Watson, 1999), central Pacific (Cooke, 1977; Gibbons & Ryland, 1989; Kirkendale & Calder, 2003) and western Pacific (Fraser, 1938; 1948; Calder *et al.*, 2003). Type locality: Gulf of Naples, Mediterranean.

REMARKS: *Pennaria disticha* is a conspicuous animal and quite well known. For the European fauna, there are no serious taxonomic problems. Its morphological variability was certainly the main reason for its complicated taxonomic history. The complete synonymy is not given here, as this has been done by Calder (1988), Hirohito (1977), García-Corrales & Aguirre (1985), and Gibbons & Ryland (1989).

Most *Pennaria* species based on the hydroid phase were synonymized with *P. disticha*, with the prominent exception of *P. wilsoni* (Hirohito, 1988; Watson, 1999).

Pennaria tiarella (Ayes, 1854), a species originally described from Long Island (New York), was already considered to be closely related to *P. disticha* by Mayer (1910). Most subsequent authors (e. g. Fraser, 1944), however, kept it separate. Also Brinckmann-Voss (1970) held it distinct from *P. disticha* on account of the variable length of the ramuli. Later authors (see above) included also *P. tiarella* in the synonymy of *P. disticha*. Weill (1937) reported a comparatively small size for the stenoteles of *P. tiarella*, but an examination of material from the same locality (BMNH 1964.8.7.5, Woods Hole) did not confirm this and the stenoteles have a maximal size that lies within the range found in other populations of *P. disticha* (see Hirohito, 1977).

The embryonic development to the planula larva has been examined in great detail by American students using animals from the USA (identified as *P. tiarella* or *P.*

disticha). Surprisingly, only few such investigations have been made using Mediterranean animals and there is an unresolved discrepancy. Cavolini (as cited in Weismann, 1883) observed that the fertilized eggs become encapsulated and overwinter as resting stages. This has never been observed again and perhaps Cavolini's observations can be attributed to the simple observation tools available at his time. Whatever, this should be re-investigated.

FAMILY CLADOCORYNIDAE ALLMAN, 1872

DIAGNOSIS: Hydroid colonial, simple stolonial or sparingly branched, hydranth club-shaped, one whorl of moniliform or capitate oral tentacles, aboral tentacles moniliform or branched capitate, scattered or in several whorls; with nematocysts on body wall arranged in conspicuous pads or scattered around the base of oral and aboral tentacles; gonophores carried singly or on short, branched pedicels on lower or middle part of hydranth; gonophores developing into free medusae or fixed sporosacs.

Medusa with two opposite perradial tentacles possessing stalked cnidophores, bell margin with four bulbs, of which two are without tentacles; above each atentaculate marginal bulb an exumbrellar pad containing macrobasic euryteles; tentaculate marginal bulbs large, without nematocyst pads; gonads interradial on manubrium.

REMARKS: The concept and relationships of the family Cladocorynidae are outlined by Petersen (1990). It comprises the genera *Cladocoryne* Rotch, 1871 and *Pteroclava* Weill, 1931.

KEY TO THE GENERA:

- 1a polyps with capitate oral tentacles; gonophores are fixed sporosacs *Cladocoryne*
- 1b polyp with moniliform oral tentacles; gonophores are free medusae
 *Pteroclava* (not in European fauna)

Genus *Cladocoryne* Rotch, 1871

TYPE SPECIES: *Cladocoryne floccosa* Rotch, 1871 by monotypy.

SYNONYMS: *Polycoryne* Graeffe, 1883a; *Cladocorynopsis* Mammen, 1963; *Lobocoryne* Mammen, 1963.

DIAGNOSIS: Cladocorynidae with long hydrocauli, these unbranched or sparingly branched, covered by perisarc. Hydranth club-shaped, with oral whorl of capitate tentacles, one to four whorls of branched-capitate aboral tentacles; on hydranth body usually nematocyst patches containing macrobasic euryteles; gonophores fixed sporosacs between or over aboral tentacles.

Cladocoryne floccosa Rotch, 1871

Fig. 16

Cladocoryne floccosa Rotch, 1871: 228; Du Plessis, 1880: 176, pl. 9; Allman, 1872: 380, fig. 82; Kühn, 1910: 69, fig. D, pl. 6 figs 28-34, pl. 7 figs 35-36; Kühn, 1913: 184, figs 28-36, pls 6-7; Philbert, 1936: 1, figs 1-8; Weill, 1937: 1, figs 1-5; Brinckmann-Voss, 1970: 69, figs 80-82; Millard & Bouillon, 1974: 11, fig. 1D-E; Millard, 1975: 65, figs 21A-B; Bouillon *et al.*, 1987: 297, figs 1 & 5-6; Hirohito, 1988: 52, figs 16 b-f; Migotto, 1996: 17, fig. 4a-b; Schuchert, 1996: 97, fig. 57a-c; Watson, 1999: 11, fig. 7A-D; Peña Cantero & García Carrascosa, 2002: 46, fig. 9e; Calder *et al.*, 2003: 1178, fig. 3; Bouillon *et al.*, 2004: 110, fig. 57G.

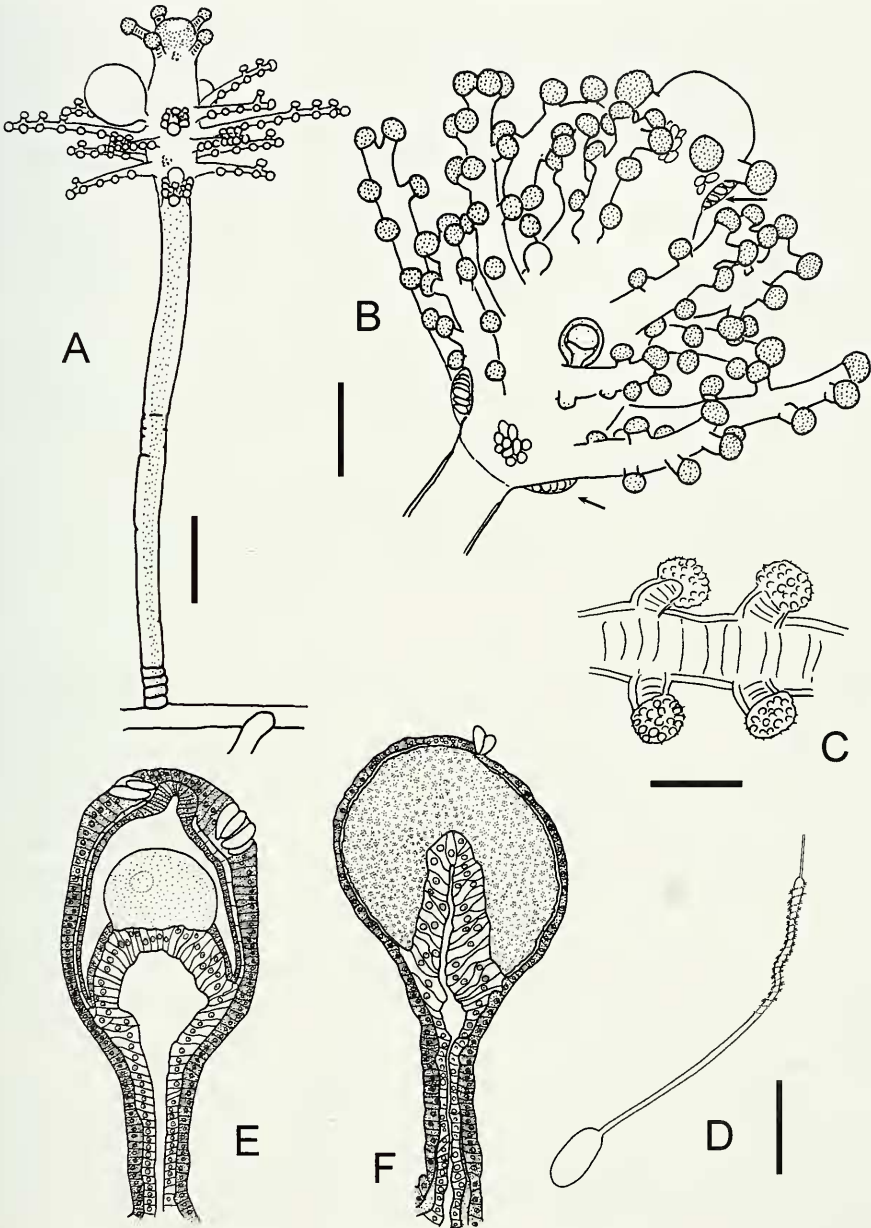


FIG. 16

Cladocoryne floccosa Rotch, 1871; A-D after preserved material from the Mediterranean; E-F, after Kühn (1910). A) Hydroid with sporesacs, scale bar 0.5 mm. B) Slightly compressed microscopic preparation of a hydranth, note position of eurytele clusters (arrows), scale bar 0.2 mm. C) Part of tentacles of aboral set, note chordoid gastrodermis, scale bar 0.1 mm. D) Macrobasal eurytele, scale bar 40 μ m. E) Histological longitudinal section of an almost mature female sporesac. F) Longitudinal section of a mature male sporesac.

Hydra corynaria Bosc, 1797.

Cladocoryne pelagica Allman, 1876: 255, pl. 10 figs 6-7.

Polycoryne helleri Graeffe, 1883a: 202, pl. figs 1-5; Graeffe, 1883b: 320, synonym.

Cladocoryne simplex Perrier, 1886: 81, fig. 3.

Cladocoryne floccosa var. *sargassensis* Hargitt, 1909: 369, figs 1-2.

Cladocoryne sargassensis – Kingsley, 1910: 19, fig. 81.

not *Cladocoryne floccosa* – Rees & Thursfield, 1965: 46 [= *C. haddoni* Kirkpatrick, 1890].

MATERIAL EXAMINED: Cala Murada, Mallorca, Spain, June 1997, on rock in 0.5-2 m depth, fertile, examined alive. – MHNG INVE 29808, Cala Murada, Mallorca, 1 m, 13 August 2000, on *Peysonnellia*, examined alive, infertile. – BMNH 1974.11.21.38, Italy, Naples, 20 April 1967, material of Brinckmann-Voss (1970), not well preserved (maceration by formalin). – MHNG INVE 36913 Naples, Cap Misene 23.01.1895, young sporosacs present, on various substrata. – MHNG INVE 36912, Villefranche-sur-Mer, infertile.

DIAGNOSIS: *Cladocoryne* species with three to four whorls of aboral tentacles, patches of macrobasal euryteles among oral and aboral tentacles, gonophores without radial canals, mature females with one to two eggs.

DESCRIPTION (after own material and literature): Hydroid with unbranched stem or rarely branched once, arising from adhering, ramified stolons. Stems covered by perisarc, smooth or with annulated stretches and becoming thinner distally to terminate below hydranth. Hydranth cylindrical to club-shaped, dome-shaped hypostome; with tentacles of two types in two well-separated sets: a single whorl of four to six short capitate oral tentacles, and 12-22 aboral tentacles in three to four alternating whorls, whorls can be indistinct. Aboral tentacles branched, side-branches short and capitate, in two lateral rows and one median row on upper side; lateral secondary tentacles up to seven per row, median row with zero to two. All side-branches and end of main branch with a terminal spherical nematocyst cluster. Sometimes some secondary tentacles without stalk and reduced to mere nematocyst clusters. Gastrodermis of tentacles chordoid. Hydranth with nematocyst patches or pads on body wall between oral tentacles and lowest aboral tentacles. Colours: hydranth light reddish brown, oral region with conspicuous white pigment.

Gonophores on short pedicels, two to eight borne on the hydranth among or above the upper aboral tentacles, spherical to oblong, remaining fixed as sporosacs without radial canals or circular canal (cryptomedusoid type), females usually with one egg only, colour white.

Nematocysts: stenoteles and macrobasal euryteles.

DIMENSIONS: Colony height a few mm to 12 mm; caulus diameter 0.15 mm; hydranth height 1-1.2 mm, diameter 0.3 mm; length aboral tentacles tentacle 0.7-1.3 mm; sporosac size: 0.3-0.4 mm. Nematocyst sizes are given in Philbert (1936); Weill (1937); Millard & Bouillon (1974); Millard (1975); Migotto (1996); Schuchert (1996); Watson (1999).

BIOLOGY: *Cladocoryne floccosa* has been reported from depths ranging from 0 to 50 m. It has often been observed on *Sargassum* weeds, but also occurs on many other solid substrata like algae, hydroids, sponges, and rocks. In the Mediterranean, it can be found from January to autumn, fertile colonies have been observed in January and from end of April to July (Brinckmann-Voss, 1970; Boero & Fresi, 1986; own observations).

ADDITIONAL DATA: Fertile animals often reduce their tentacles, sometimes leading to tentacle-less hydranths (reproductive exhaustion). Kühn (1910) describes the formation of the gonophores and the gametogenesis. The mature female sporosacs usually contain one egg only. Initially there are many eggs, but during the maturation one of them phagocytoses all the others. The embryonic development takes place in the sporosac. Philbert (1936) depicts the metamorphosis of the larva to the primary polyp. The nematocysts are depicted in Weill (1937). A longitudinal section of a hydranth is depicted Prévot (1959) and in Bouillon *et al.* (1987, fertile hydranth). Peña Cantero & García Carrascosa (2002) found branched stems that had up to four hydranths.

DISTRIBUTION: Circumglobal in temperate to tropical waters. Along the European coasts known from north-west of Ireland (Allman, 1876, as *C. pelagica*), the English Channel (Rotch, 1871; Philbert, 1936; Teissier, 1965), the Iberian Peninsula (Da Cunha, 1944; Medel & López-González, 1996), western Mediterranean (Du Plessis, 1880; Motz-Kossowska, 1905; Brinckmann-Voss, 1970; Peña Cantero & García Carrascosa, 2002; and more), eastern Mediterranean (Picard, 1958; Morri & Bianchi, 1999). Also known from the western Atlantic (Hargitt, 1909 as *Cladocoryne floccosa* var. *sargassensis*; Migotto, 1996); the Indian Ocean (Millard & Bouillon, 1974; Watson, 1999); the western Pacific (Hirohito, 1988; Schuchert, 1996); the eastern Pacific (Lees, 1968; Calder *et al.*, 2003). Type locality: on stones at low tide at Herm, Guernsey, Channel Islands, United Kingdom.

REMARKS: This is a characteristic species that cannot be confounded with any other hydroids of the European fauna. The synonymy is quite well established. *Polycoryne helleri* Graeffe, 1883a was recognized as a synonym by Graeffe (1883b) himself. *Cladocoryne pelagica* Allman, 1876 was described based on a fertile colony found on floating *Sargassum* seaweed northwest of Ireland. Allman kept it distinct on account of its smaller size and the annulated base of the pedicel. These traits are no longer considered diagnostic and in his revision, Philbert (1936) regarded it as a synonym of *C. floccosa*, likewise also *C. simplex* Perrier, 1886, and *C. haddoni* Kirkpatrick, 1890. Most subsequent authors took up Philbert's conclusion, but Bouillon *et al.* (1987) re-described *C. haddoni* based on material from Papua New Guinea and found sufficient differences to *C. floccosa* to permit a reliable identification, even of immature specimens. *Cladocoryne haddoni* was therefore recognized as a distinct species. *Cladocoryne pelagica*, *C. simplex* and *C. sargassensis* are very likely conspecific with *C. floccosa*, although the original descriptions are usually not detailed enough. A re-examination of the type material of *C. pelagica* and a detailed examination of *Cladocoryne* hydroids on *Sargassum* would therefore be helpful. Calder *et al.* (2003) discovered another likely synonym of *C. floccosa*, namely *Hydra corynaria* Bosc, 1797, a *Cladocoryne* species that was also originally described based on material growing on *Sargassum*. Because Bosc's name has not been used since its original description Calder *et al.* (2003), based on provisions of the ICZN, invalidated Bosc's name and to declared *Cladocoryne floccosa* Rotch, 1871 a protected name.

FAMILY CLADONEMATIDAE GEGENBAUR, 1856

SYNONYMS: Cladonemiden Gegenbaur, 1856; emended to Cladonematidae by Poche (1914: 70); Stauriidae Hincks, 1868; Dendronemidae Haeckel, 1879; Eleutheriidae Stechow, 1923.

REFERENCES: Günther (1903), Hartlaub (1887), Stechow (1923), Bouillon (1985), Calder (1988), Petersen (1990), Bouillon & Boero (2000).

DIAGNOSIS: Hydroid colony stolonial or rarely sparingly branched, arising from creeping stolons. Hydranth spindle-shaped, one whorl of four to ten solid oral capitate tentacles, with or without aboral whorl of filiform tentacles; mouth opening into a pre-oral chamber formed by epidermal gland cells; medusa buds not enclosed in periderm film, carried singly or in clusters at base of hydranth or above filiform tentacles if they are present.

Medusa adapted to benthic mode of life, some species still able to swim freely; with or without a thickened continuous or broken ring of nematocysts around umbrella margin, with or without brood-chamber above manubrium; manubrium cylindrical, with or without protruding pouches; mouth either simple, or with oral nematocyst clusters, or with ramified oral tentacles; gonads either completely surrounding manubrium, or on manubrial pouches, or in special brood-chamber above manubrium, in latter case also sometimes additionally in subumbrellar epidermis; number of radial canals variable but usually more than four, some may be branched, final number of canals entering circular canal usually corresponding or slightly exceeding the number of marginal tentacles; marginal tentacles hollow, branched, with branches bearing nematocyst clusters and branches having adhesive organs; with abaxial ocelli on tentacle base.

REMARKS: As some Cladonematidae can be cultivated quite easily, they have become the subject of numerous developmental and molecular studies. They thus became quite well known even to non-specialists. The European Cladonematidae species present few taxonomic problems and the species are mostly well known, though the genus *Dendronema* remains problematic. However, taxonomic problems persist at the genus level.

The family Cladonematidae has been kept separate from the Eleutheriidae Stechow, 1923 by a number of authors (for more details see Calder, 1988). The latter family comprised the genera *Staurocladia* and *Eleutheria*. The separation of both families is ambiguous and not necessary and the proposal of Petersen (1990) to unite them is here also adopted. A good example in favour of this is *Staurocladia portmanni* Brinckmann, 1964, which is perfectly intermediate between *Staurocladia* and *Cladonema*, differing basically only in the branching of the tentacles. The genera *Cladonema*, *Staurocladia*, and *Eleutheria* are linked by a number of synapomorphic characters, such as the preoral chamber in the hydroid, the branched medusa tentacles with adhesive ends, and the number of radial canals (Petersen, 1990).

In current usage (Kramp, 1961; Bouillon, 1985; Bouillon & Boero, 2000), the family comprises four genera: *Cladonema*, *Dendronema*, *Staurocladia*, and *Eleutheria*. *Dendronema* is somewhat problematic and the distinction of the three remaining genera relies principally only on the morphology of the capitate tentacles of the medusa. *Cladonema* has tentacles that are branched more than once and its umbrella is not reduced. In *Staurocladia*, the tentacles are only bifid and the upper branch bears additional nematocyst clusters besides the terminal one. *Eleutheria* was diagnosed as having bifid tentacles with a single terminal nematocyst cluster, and additionally a

brood-chamber above the manubrium. There remain, however, problems with this classification, especially so for the scope of *Staurocladia*.

Hartlaub (1917) established the genus *Staurocladia* solely to separate *Eleutheria vallentini*, *E. claparedii*, and others from *Eleutheria dichotoma*. He found this necessary to account for some of the peculiarities of *E. dichotoma*: the brood-chamber, the hermaphroditism, and the gonostyle in the polyp phase. Hartlaub therefore used the combination *Staurocladia claparedii* (Hartlaub, 1889), as this species has no brood-chamber (Müller, 1911; Lengerich, 1923a). Lengerich (1923a) used only a single genus, *Eleutheria*, for all Cladonematidae. Although this would resolve the problem of paraphyletic genera, it creates unwanted name changes for widely known species. Probably unaware of Hartlaub's publication, Gilchrist (1919) had similar thoughts and suggested the genus name *Cnidonema* for the *Eleutheria* species of the southern hemisphere. He also thought that it might be necessary to introduce a new genus for *E. claparedii* if this species should have no brood-chamber. Browne & Kramp (1939) and Kramp (1959, 1961, 1968) took up Hartlaub's diagnosis, but modified the definition so that *Staurocladia* was differentiated from *Eleutheria* by the number of nematocyst clusters per tentacle (*Eleutheria* one, *Staurocladia* more than one) and the absence or presence of a brood-chamber. Browne & Kramp (1939) placed *E. claparedii* in the genus *Eleutheria*, because they were probably unaware that it has no brood-chamber. Brinckmann-Voss (1970) became aware of this discrepancy and changed the genus diagnosis of *Eleutheria* accordingly to "with or without brood-chamber above manubrium". The genera *Staurocladia* and *Eleutheria* were hence distinguished only on account of the number of nematocyst clusters. However, later authors reverted to Kramp's (1961) diagnosis (e. g. Bouillon, 1985; Petersen, 1990; Bouillon & Boero, 2000), but were inconsistent in placing *E. claparedii* in the genus *Eleutheria*.

Distinguishing a genus solely on the number of tentacular nematocyst clusters appears quite ambiguous and very prone to give polyphyletic assemblages. It is thus quite unlikely that the present genera correspond to a monophyletic groups. Unfortunately, there are few useful characters for a phylogenetic analysis of the members of the Cladonematidae. Synapomorphies that can be used to find species groupings are given in table 1. There are more apomorphies, but either they are autapomorphies (gonostyle, very extensible hydranth, brood-chamber, centripetal canals, radial canals with processes, apical cavity), or only examined for one or few species (desmonemes in polyp stage, heteronemes in polyp stage). Some characters are not really usable (lateral or aboral position of nematocyst clusters).

Using these characters for a cladistic analysis of representative members of the family was not very helpful (table 1, figure 17). There are several unresolved polytomies, but it is worth mentioning that *Staurocladia* is evidently a polyphyletic group. In this case, it seems nevertheless prudent not to use these results to redefine the genera because taxonomic stability should be given more value than a classification based on a poorly resolved cladogram. Perhaps a thorough molecular analysis can provide the necessary data, but until then, the diagnoses for *Eleutheria* and *Staurocladia* as given in Brinckmann-Voss (1970) should be used.

TABLE 1
 Characters used in the phylogenetic analysis of the genera of the Cladonematidae

Species / Characters	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Dipirena reesi</i> Vannucci, 1956	1	0	0	0	0	0	0	0	0	0	1	0	0
<i>Dipirena strangulata</i> McCrady, 1859	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cladosarsia minima</i> Bouillon, 1978	?	?	0	0	0	0	0	0	0	1	1	0	0
<i>Cladonema radiatum</i> Dujardin, 1843	1	1	0	1	1	1	1	1	0	1	1	0	0
<i>Dendronema stylodendron</i> Haeckel, 1879	?	?	0	1	1	1	1	1	0	1	1	0	0
<i>Eleutheria dichotoma</i> Quatrefages, 1842	1	1	1	1	1	0	0	0	1	0	0	1	1
<i>Eleutheria claparedii</i> Hartlaub, 1889	0	?	1	1	1	0	0	0	1	0	0	0	1
<i>Staurocladia portmanni</i> Brinckmann, 1964	1	1	0	1	1	1	1	1	0	0	1	0	0
<i>Staurocladia valleritini</i> (Browne, 1902)	1	1	1	1	1	0	0	0	1	0	1	1	1
<i>Staurocladia wellingtoni</i> Schuchert, 1996	0	1	1	1	1	1	1	1	0	0	1	0	0

characters:

- 1 polyp: filiform tentacles: none (0), present (1)
- 2 polyp: gonophore without perisarc film (1)
- 3 mesogloea rigid, medusa thus able to swim freely (0), not so (1)
- 4 medusa tentacles with adhesive ends; absent (0), present (1)
- 5 four radial canals (0), more than four (1)
- 6 radial canals unbranched (0), branched (1)
- 7 oral knobs absent (0), present (1)
- 8 manubrial pouches absent (0), present (1)
- 9 medusae budding absent (0), present (1)
- 10 tentacles branched more than once, no (0), yes (1)
- 11 medusa one terminal nematocyst cluster per tentacle only (0), additional clusters present (1)
- 12 continuous marginal nematocyst ring absent (0), present (1)
- 13 tentacles and radial canals in phase (0), out of phase (1)

note: the character "preoral chamber", likely an apomorphy for the Cladonematidae, was not used, because its state is known for three species only (*C. radiatum*, *S. portmannii*, *E. dichotoma*)

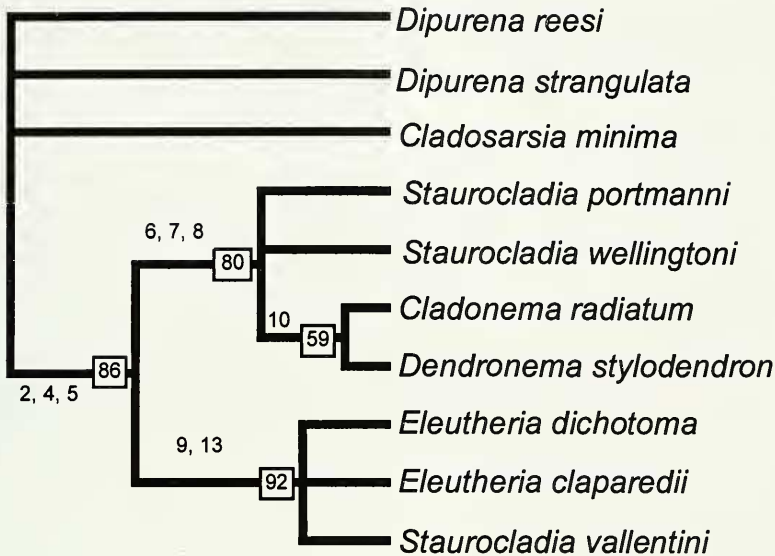


FIG. 17

Genera of the Cladonematidae: Phylogenetic analysis of morphological characters using maximum parsimony: Strict consensus tree of the 17 trees with minimal length (18 steps, HI=0.28, CI=0.72, RI=0.81). The consensus tree of the bootstrap analysis was identical, the percentage of node support is given in boxes. Some selected synapomorphies are also given (numbers along branches, see table 1).

KEY TO THE CLADONEMATIDAE:

- 1a medusa tentacles branched more than once 2
 1b medusa tentacles branched once 3
 2a oral nematocyst knobs of medusa simple *Cladonema*
 2b oral nematocyst knobs of medusa branched *Dendronema*
 3a medusa tentacles with a single nematocyst knob *Eleutheria*
 3b medusa tentacles with a several nematocyst knobs *Staurocladia*

Genus *Cladonema* Dujardin, 1843

TYPE SPECIES: *Cladonema radiatum* Dujardin, 1843 by monotypy.

SYNONYMS: *Stauridia* Forbes, 1848; *Stauridium* Krohn, 1853b.

REFERENCES: Kramp (1961); Bouillon (1985); Calder (1988); Petersen (1990); Bouillon & Boero (2000).

DIAGNOSIS: Hydroid mostly stolonial, occasionally branched, one oral whorl of four to five capitate tentacles, with or without filiform tentacles, medusa buds borne singly on hydranth body immediately above filiform tentacles or in similar position when these are absent. Medusae adapted for swimming and adhering to surfaces, with bell-shaped umbrella; manubrium cylindrical, in adults with pouches, gonads without perradial separations, mouth short, unbranched lips bearing four to six spherical nematocyst clusters; without apical chamber above manubrium; radial canals bifurcated or simple, final number of canals entering circular canal usually of same number

as marginal tentacles; marginal tentacles branching, each with one to six proximal branches ending in an adhesive organ and one to ten more distal branches with nematocyst clusters; abaxial ocelli with lens.

Cladonema radiatum Dujardin, 1843

Fig. 18

Cladonema radiatum Dujardin, 1843: 1134; Dujardin, 1845: 271, pl. 14 figs C1-C7, pl. 15 figs C8-C19; Krohn, 1853b: 420, pl. 13; Keferstein & Ehlers, 1861: 85, pl. 13 fig. 5; Van Beneden, 1867: 139, pl. 12; Hincks, 1868: 62, text fig. 5, pl. 11; Allman, 1871-1872: 216, pl. 17; Hincks, 1872: 391, pl. 21, fig. 6; Hartlaub, 1887: 266, 651; Billard, 1905: 500; Hartlaub, 1907: 132, figs 123-126; Müller, 1908: 30, pl. 3 figs 1-2; Mayer, 1910: 99, figs 53-55; Lengerich, 1923a: 331, figs A-S; Weill, 1937: 443, fig. 1; Russell, 1953: 105, figs 49-51; Kramp, 1959: 96, fig. 55; Brinckmann & Petersen, 1960: 388, fig. 2; Kramp, 1961: 57; Kramp, 1968: 22, fig. 52; Naumov, 1969: 245, figs 113, 117A-H; Brinckmann-Voss, 1970: 76, figs 88-89, pl. 5 figs 1-2; Bouillon, 1971: 333, figs 4.5-7; Millard & Bouillon, 1973: 12, fig. 1A; Rees, 1979: 300; Calder, 1988: 67, fig. 50; Hirohito, 1988: 41, fig. 12a-b; Schuchert, 1996: 131, fig. 80a-d; Migotto, 1996: 23, fig. 4e-g; Bouillon *et al.*, 2004: 88, fig. 48B-D.

Coryne stauridia Gosse, 1853d: 257, pl. 16 figs 1-5.

Syncoryne stauridium Krohn, 1853a: 137.

Cladonema Gegenbauri Haeckel, 1879: 109.

Cladonema Krohnii Haeckel, 1879: 109.

Cladonema Dujardinii Haeckel, 1879: 109.

Cladonema Allmani Haeckel, 1879: 109.

Stauridium cladonema Haeckel, 1879: 109.

Cladonema perkinsii Mayer, 1904: 18, pl. 4 fig. 35; Mayer, 1910: 101, pl. 9 fig. 1.

Cladonema mayeri Perkins, 1906: 118; Mayer, 1910: 101, pl. 9 figs 2-3.

Stauridia radiatum – Mayer, 1910: 100.

Eleutheria radiata – Lengerich, 1922: 210, fig. 1; Lengerich, 1923a: 313, figs G-S.

? *Cladonema novae-zelandiae* Ralph, 1953: 72, fig. 20.

MATERIAL: Aquarium culture of polyp stage originating from the Mediterranean, 18 January 1991, life-cycle observed to mature medusa. – MHNG INVE 29909, Roscoff, Brittany, polyps on holdfast of laminarian, collected 1 June 2001, cultured at room temperature, medusae buds developed, very cold-sensitive, died at <14°, grew well at 22-30°C; 16 S sequence accession number AY512539. – Three medusae, Bay of Portoferraio, Island of Elba, Italy, collected July 2005 by dragging a plankton net over a *Posidonia* meadow, depth 2-4 m; colour of whole medusa light brown, 16 S sequence accession numbers of two different individuals AM088482 and AM088483. – MHNG INVE 37640, 19 February 2004, polyps on "living stones" from tropical aquarium, origin unknown, medusae cultivated to near maturity, 16 S sequence accession number AM088484, appeared identical to other *C. radiatum* medusae except that proximal parts of radial canals were white, also on manubrium longitudinal stripes of white pigment; this material belongs thus perhaps to a separate species of tropical origin, a fact also suggested by the deviating 16S sequence.

DIAGNOSIS: Hydroid with one oral whorl of capitate tentacles, each with up to ten gastrodermal cells, with one aboral whorl with usually four filiform tentacles. Medusa tentacles branched several times, two and more adhesive branches in fully mature animals, two and more capitate branches; manubrium shorter than bell cavity, mouth with four to five spherical nematocyst clusters, gonads on manubrial pouches and on manubrium, radial canals bifurcated or not.

DESCRIPTION: Hydroid colonies stolonal or rarely branched, arising from creeping, ramified stolons, hydranths on pedicel of variable length, but usually longer than hydranth. Perisarc smooth, terminating shortly below filiform tentacles.

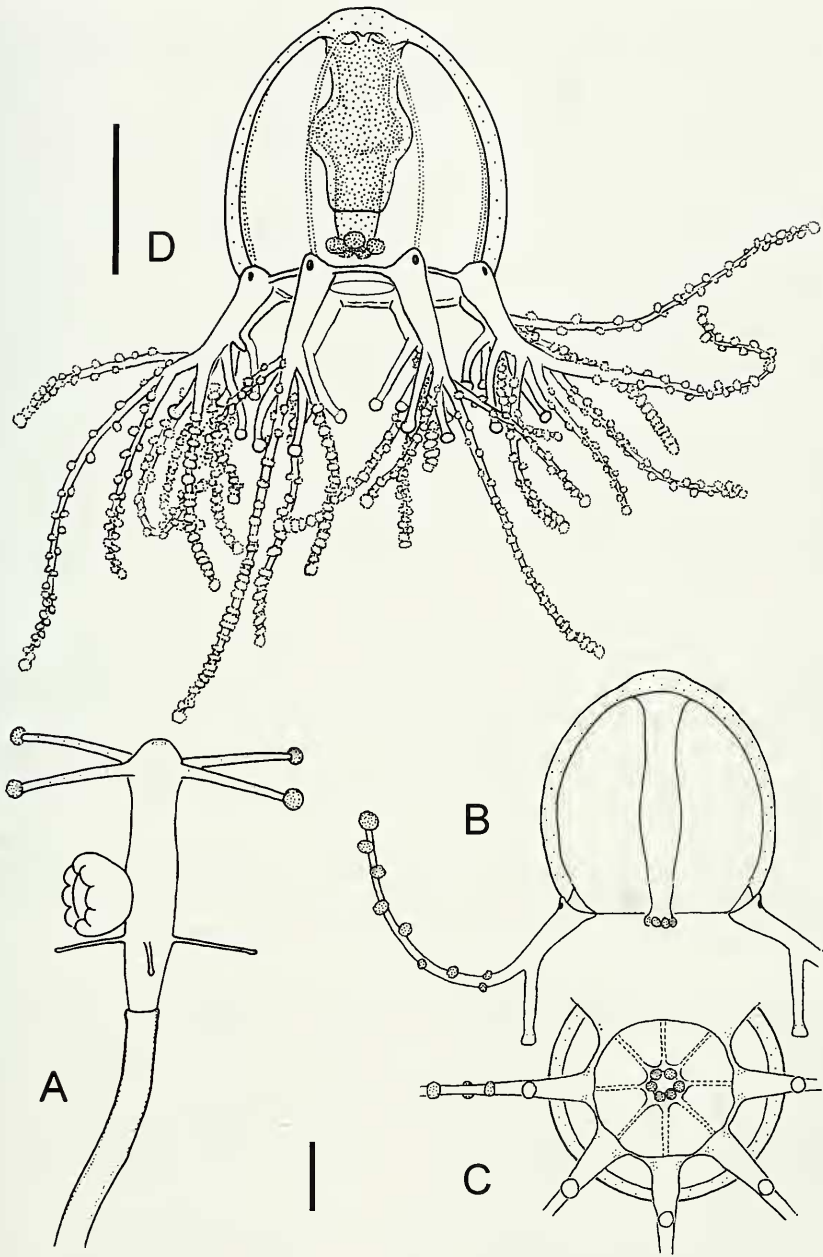


FIG. 18

Cladonema radiatum Dujardin, 1843. A-C, after living material from Brittany; D, after photos of living Mediterranean medusae. A) Polyp with medusa bud, scale bar 0.2 mm. B) Lateral view of newly released medusa in optical section, same scale as A. C) Oral view of newly released medusa. D) Mature male medusa, scale bar ca. 1 mm.

Hydranths with one oral whorl of four to five capitate tentacles, each tentacle with seven to ten chordoid gastrodermal cells. Below capitate tentacles one whorl of four (occasionally five) slender, filiform tentacles with a slight terminal swelling, without nematocysts. Hypostome with an epidermal preoral chamber. Medusae buds naked, arising above filiform tentacles. Nematocysts: stenoteles and mastigophores.

Newly released medusa with eight to ten bifid tentacles, upper branch with a terminal nematocyst cluster and a few oral-aboral clusters (Fig. 18).

Adult medusa with bell-shaped umbrella, slightly higher than wide, jelly moderately thin, sometimes with a slight apical projection, velum rather broad. Medusa able to swim freely but mostly remains attached, does not move by crawling. Manubrium spindle-shaped, shorter than or as long as bell cavity, with five (sometimes four or six) perradial pouch-like protuberances in its middle region, protuberances rather shallow, size variable. The gonads completely surround the upper two thirds of manubrium inclusive the pouches. Mouth with four to five bulbous nematocyst clusters. Radial canals may bifurcate close to the manubrium and eight to ten canals reach the circular canal, branching pattern variable even in individuals from the same colony. Number of marginal tentacles corresponds to the number of radial canals. Each tentacle base with an abaxial ocellus. Marginal tentacles branched, with elongated thickened base and a long main branch from the underside of which grow one to six short tentacles acting as adhesive organs, the ends of the adhesive tentacles have a distinct spherical swelling at their end; distal to the adhesive branches the main branch gives off up to five side-branches bearing nematocyst clusters alternating in aboral and oral position and one larger terminal cluster, proximal side-branches originate orally, more distal ones issuing laterally from the main branch. Colour of stomach and marginal tentacles red, bright-red or brown; ocelli black or deep crimson. Nematocysts: stenoteles, desmonemes.

DIMENSIONS: Hydroid colonies up to 25 mm, hydranth about 1 mm; newly released medusa 0.7-1.0 mm, adult medusa up to 3 mm high. Nematocysts see Weill (1936), Brinckmann & Petersen (1960), Schuchert (1996).

BIOLOGY: For Mediterranean populations, Brinckmann-Voss (1970) reports that the polyp colonies remain small in nature (2-3 hydranths), they were found in shaded places on algae and other hard substrata. From end of June to the end of July, the medusae were caught in large numbers in *Posidonia* beds, later they are rare or absent. The development of the medusae-buds is quick, at 18°C it takes only 6-7 days until the medusa is set free. Also Motz-Kossowska (1905) observed the medusae only from June to August, rarely also in October.

ADDITIONAL DATA: The polyps of *Cladonema radiatum* are easy to keep in laboratory. Dujardin (1843) kept them for several years, Lengerich (1923a) reports a colony that was kept for more than 30 years in an aquarium in Berlin. Also the medusa is relatively easy to keep and reaches maturity in culture vessels. It also turns up regularly in aquariums. It is thus an ideal experimental organism and therefore there is a large number of developmental and histological investigations which cannot be reviewed here in detail.

The morphology, histology, and ultrastructure was dealt with in detail by e. g. Müller (1908); Lengerich (1923a; 1923b), Brien (1942), Bouillon (1968), Bouillon & Houvenaghel (1970), Tardent & Stössel (1971), Weber & Tardent (1978), Weber (1980, 1981a, 1981b), Bouillon *et al.* (1988), Falugi *et al.* (1994).

The nematocysts and their biology were investigated by: Weill (1936), Brien (1942), Achermann & Tardent (1973), and Bouillon (1971).

The development and medusae budding was investigated by e. g.: Pasteels (1939, 1941), Brien (1941, 1942), and Bodo (1970).

The behaviour of the medusa is described by: Allman (1872), Browne (1900), Billard (1905), Lengerich (1923a), and Russell (1953, summary). It is important to note in this context that the medusa does not crawl like *Eleutheria dichotoma*, but changes place by swimming. The adhesive tentacles are thus only used for clinging to a surface. There is also a differences in the ultrastructure of the adhesive tentacles (Bouillon, 1968).

The medusae can be hermaphroditic, but usually this is rare (Hartlaub, 1887; Müller, 1908; Bouillon & Houvenaghel, 1970). Bouillon & Houvenaghel (1970) found only two hermaphroditic animals among fifty medusae, while others observed none (Lengerich, 1923a). They can be successive hermaphrodites beginning either as females or males (Hartlaub, 1887).

DISTRIBUTION: North-Eastern Atlantic: Norway (Christiansen, 1972), Great Britain and Ireland (Hincks, 1868; Allman, 1872; Russell, 1953), Sweden (Segerstedt, 1889; Aurivillius, 1898; Kramp, 1935); Denmark (Kramp, 1935); Helgoland (Richters, 1908); Holland (Vervoort, 1946), Belgium (Leloup, 1947), Atlantic coast of France (Dujardin, 1843; Billard, 1905; Teissier, 1965), Atlantic coast of the Iberian Peninsula (Medel & López-González, 1996). Mediterranean (numerous records, e. g. Brinckmann-Voss (1970), Boero & Fresi (1986), Daly Yahia *et al.* (2003, Tunisia), Bouillon *et al.* (2004)). Present in the Black Sea (Thiel, 1935). Also known from Brazil (Migotto, 1996), Bermuda (Calder, 1988), Indian Ocean (Millard & Bouillon, 1973), ? New Zealand (Schuchert, 1996), Japan (Hirohito, 1988; introduced?). Type localities: Dujardin (1843) described material from the Mediterranean, St. Malo, and Lorient (France).

REMARKS: The medusa of *Cladonema radiatum* is quite variable with respect to the number and branching patterns of the radial canals. Also the number of adhesive tentacles, manubrial pouches, and oral nematocyst clusters is variable in natural populations. Even monoclonal animals show some degree of variation.

Weill (1937) examined 106 specimens collected at Bermuda and these encompassed the characteristics of *C. radiatum*, *C. perkensii*, and *C. mayeri*. Weill concludes that the three nominal species were no more than varieties of one rather variable species, as Mayer (1910) had suggested earlier. This view has been adopted by most subsequent authors (e. g. Russell, 1953; Kramp, 1959; Kramp, 1961).

There are several nominal *Cladonema* species known, but sometimes the differences to *C. radiatum* are unclear or minimal (Kramp, 1968). Rees (1979) and Stepanjants *et al.* (1993) review all the differences between the different nominal species. Stepanjants *et al.* (1993) concluded that there were only two valid species, namely *C. radiatum* and *C. californicum*.

The medusae of *Cladonema californicum* Hyman, 1947 was held distinct from all other described *Cladonema* in having only one adhesive tentacle branch and one to two nematocyst bearing branches, and a manubrium that protrudes from the velar opening (Hyman, 1957; Rees, 1979). According to Hyman (1957), the gonads cover the manubrium on the pouches and the rest of the manubrium, this in contrast to the diagnosis in Kramp (1968). The polyp appears indistinguishable from *C. radiatum*.

The polyps of the Californian *Cladonema myersi* Rees, 1949 lack filiform tentacles, the medusa lacks branching radial canals, and the gonad covers the entire manubrium (Naumov, 1969). Likewise, the polyps of the Japanese *Cladonema uchidai* Hirai, 1958 also lack filiform tentacles.

Naumov (1955) described *Cladonema pacificum*, which he later (1960, 1969) synonymized with *C. myersi*. This was contested by Hirohito (1988). Rees (1979) and Hirohito (1988) think that *C. uchidai* belongs to *Cladonema pacificum*. This species is distinguished from *C. radiatum* by a gonad that covers almost the whole manubrium, and not only the upper 2/3 (compare Bouillon *et al.*, 1988: fig. 1).

Cladonema novaehelandiae Ralph, 1953 has been synonymized with *C. radiatum* by Schuchert (1996). However the polyp stage of the New Zealandic *Cladonema* remains unknown and it may turn out to be different from *C. radiatum*. Its synonymy with *C. radiatum* is therefore not sufficiently established.

Although it is evident that many nominal *Cladonema* species are currently not objectively distinguishable, it is still likely that several distinct biological species have been included in *C. radiatum*. The 16S sequences of the *Cladonema* sample found in aquarium with tropical material (see above in material examined) differs in more than 25% of its positions from the Atlantic and Mediterranean sequences. Such a difference represents more likely interspecific variation (comp. Schuchert, 2005). The differences among the examined European sequences are less than 4%.

The hydroid of *Cladonema radiatum* is rather difficult to distinguish from hydroids of some Corynidae (Schuchert, 2001b). Brinckmann & Petersen (1960) found that the number of gastrodermal cells in the capitate tentacles offers a reliable tool to discriminate *Cladonema radiatum* and *D. reesi*: while *C. radiatum* has 10 or less cells, *D. reesi* has 13-18 (see also Schuchert, 2001b). Additionally, the macrobasic heteroneme is characteristic for *Cladonema radiatum*. Also the hydroid of *Staurocladia portmanni* is very similar. Brinckmann-Voss (1970) found that *S. portmanni* polyps have regularly six filiform tentacles, while *C. radiatum* has usually four, sometimes five.

Genus *Eleutheria* Quatrefages, 1842

TYPE SPECIES: *Eleutheria dichotoma* Quatrefages, 1842, by monotypy.

SYNONYMS: *Clavatella* Hincks, 1861; *Herpusa* Schmidt, 1869.

REFERENCES: Kramp (1961); Bouillon (1985); Petersen (1990); Bouillon & Boero (2000).

DIAGNOSIS: Hydroid with an oral whorl of up to ten capitate tentacles, without aboral filiform tentacles; medusae buds carried in clusters on short blastostyles (gonostyle) or singly at base of hydranth. Medusae adapted for crawling, unable to swim; umbrella with or without continuous ring of nematocysts along margin; with four or

more simple and short radial canals; manubrium with broad base, conical, with simple circular mouth; with or without brood-chamber above base of stomach; gonads either on manubrium, or in brood-chamber from where they can also extend to the epidermis of the subumbrella; 6-14 bifurcated marginal tentacles, one upper branch with a single terminal nematocyst knob, one lower branch with adhesive organ: asexual reproduction through medusa budding present.

REMARKS: The problems concerning the distinction of *Eleutheria* and *Staurocladia* have been discussed above under remarks at the family level.

KEY TO THE EUROPEAN *ELEUTHERIA* MEDUSAE:

- 1a medusa buds on outside, with brood-chamber *Eleutheria dichotoma*
 1b medusa buds in subumbrella, no brood-chamber *Eleutheria claparedii*

Eleutheria dichotoma Quatrefages, 1842

Figs 19A-C, 20

Eleutheria dichotoma Quatrefages, 1842a: 270, pl. 8; Quatrefages, 1842b: 168; de Filippi, 1866: 375, pl. 1; Hartlaub, 1886: 706, text. fig.; Hartlaub, 1907: 127, figs 119-120; Mayer, 1910: 94, figs 46-48; Müller, 1908: 34, pl. 3 figs 3-7, pl. 4; Lengerich, 1923a: 359, figs R'-Z', D2; Drzewina & Bohn, 1913: 49, figs 26-37; Weill, 1936: 816; Russell, 1953: 110, figs 52-53; Kramp, 1961: 59; Naumov, 1969: 249, figs 118-121; Brinckmann-Voss, 1970: 79, figs 90-92; Bouillon, 1994: 146, fig. 55; Bouillon, *et al.* 2004: 88, fig. 48B-D.
Clavatella prolifera Hincks, 1861: 73, pls 7-8; Hincks, 1868: 73, pl. 12 fig. 2; Allman, 1872: 384, pl. 18.

Herpusa ulvae O. Schmidt, 1869: 993, fig.

Eleutheria tetranema Haeckel, 1879: 106.

Eleutheria pentanema Haeckel, 1879: 106.

Eleutheria hexanema Haeckel, 1879: 106.

Eleutheria anisonema Haeckel, 1879: 106.

Eleutheria heptanema Haeckel, 1879: 107.

Eleutheria octonema Haeckel, 1879: 107.

Eleutheria dichocnida Haeckel, 1879: 107.

Eleutheria cnidobdella Haeckel, 1879: 107.

Eleutheria dichobdella Haeckel, 1879: 107.

Eleutheria heteroclada Haeckel, 1879: 107.

Cladonema prolifera – Motz-Kossowska, 1905: 47.

Eleutheria krohni Krumbach, 1907: 453.

Eleutheria gemmipara Du Plessis, 1909: 376.

not *Eleutheria dichotoma* – Claparède, 1863: 4, pl. 1 figs 4-10 [= *E. claparedii*].

not *Eleutheria dichotoma* – Spagnolini, 1876: 312 [= *E. claparedii*].

MATERIAL: MHNG INVE 34228, Mediterranean, Banyuls-sur-Mer, île Grosse, 2 May 2002, 0 m, > 10 medusae on *Ulva lactuca*, with eggs/planulae in brood-chamber, examined alive, development to primary polyp followed, DNA sample deposited, 16S sequence accession number AM088485. – MHNG INVE36841 living polyp colony obtained from B. Schierwater, collected 1995, Spain, Tossa de Mar, La Fosca, medusae buds developed after a few days of cultivation.

DIAGNOSIS: *Eleutheria* medusa with brood-chamber, medusae buds outside on bell rim or exumbrella, normally six tentacles, tentacles bifurcated once in middle, trunk and branches of about the same length, often hermaphroditic, nettle ring thick.

DESCRIPTION: Hydroid stolonial, stolons creeping, branched, perisarc smooth; hydranths with very short pedicels, sometimes almost sessile, pedicel covered by thin periderm, sometimes widened like a funnel. Hydranth body cylindrical, very extensile, fully extended with very thin body and swollen terminal region, one oral whorl of four

to eight capitate tentacles, 16-18 gastrodermal cells per tentacle. Filiform tentacles absent. Medusae buds in lowest part of hydranth, either singly or in clusters borne on short gonostyle (tubular outgrowth of body wall, up to four per hydranth), gonostyles branching or not, carrying up to four medusae buds, buds not protected by periderm covering. Preoral cavity visible in living animals. Colour: gastrodermis white or pink, depending on food.

Medusa umbrella somewhat flattened-hemispherical, with its oral surface more or less six-sided and with well-developed thickened marginal ring packed with nematocysts. Velum broad, usually closing umbrella and opened only when feeding. Manubrium broadly conical, filling almost the entire subumbrella, extensible beyond umbrella, mouth simple and without nematocyst knobs. Gonads in specialized cavity or brood-chamber situated above the manubrium, often male and female gametes present, female gonads in lower epithelium of brood-chamber, male gonads in upper epithelium, and also on subumbrella, embryos develop in brood-chamber, up to seven planulae can be present. Radial canals very short, usually six in number. Ring canal relatively large, widening at junctions with radial canals. Tentacles hollow proximally, chordoid distally, mostly six or five present, but rarely also other numbers possible, bifurcated at about middle, upper branch only with one terminal nematocyst cluster, lower branch terminating in adhesive organ used to cling to the substratum. One abaxial ocellus on base of each tentacle. Medusae budding from bell margin and lower part of exumbrella regularly present, also in reproductive animals. Colours: body olive-cream, ocelli red to brown. Nematocysts: polyp with stenoteles of two size classes; medusa with stenoteles and desmonemes.

DIMENSIONS: Polyp 1-6 mm and more, very contractile; tentacular capitula diameter 0.25-0.30 mm. Medusa bell diameter 0.4-0.8 mm, tentacle length 1.8 mm. Egg size 47-93 μm (Tardent, 1978). Stenoteles of polyp: (30-33.5)x(19-21) μm and (16.5-18.5)x(9-11) μm . Stenoteles of medusa: (12-24)x(7-16) μm , apparently not falling into distinct, different size classes. Desmonemes of medusa: (7.5-9.5)x(4-5) μm .

DISTRIBUTION: Present along all coasts of Europe and the Mediterranean, rarer in the southern North Sea, perhaps absent in the Baltic Sea. Also known from the Black Sea (Thiel, 1935), Madeira (Friedrich, 1961), and the Caribbean (Spracklin, 1982). The northernmost occurrence seems to be near Bergen in Norway (Kramp & Damas, 1925). Records for the Swedish west coast are given by Hartlaub (1886), for the British Isles by e. g. Hincks (1861, 1868), Allman (1872), for France by e. g. Drzewina & Bohn (1913) and Teissier (1965), for the Atlantic coast of Spain by Medel & López-González (1996). The Mediterranean records are summarized in Brinckmann-Voss (1970). Type locality: Chausey Isles, English Channel.

BIOLOGY: The polyp has only rarely been found in nature. Hincks (1868) observed that in England medusae budding takes place during summer and autumn. The medusa lives attached to various seaweeds, preferably on *Ulva* species, but also on *Cystoseira*, *Gelidium* and other substrata. It lives in shallow depths, also frequently in tide pools. Brinckmann-Voss (1970) found the medusa also in deeper waters (20 m). Sexual reproduction in the English Channel was observed in May to June and October to November (Teissier, 1965).

ADDITIONAL DATA: *Eleutheria dichotoma* is easy to keep in small containers and it has therefore been a favourite subject for a number of studies. Hartlaub (1886) examined the formation of the brood-chamber in histological sections. The subumbrellar epidermis forms canal-shaped cavities that penetrate the region above the stomach. The fusion of these canals in the centre then creates the brood-chamber. The brood-chamber is connected to the subumbrella by interradial openings (thus usually six). The gastrodermis of the manubrium becomes completely separated from the umbrella. The eggs mature in the lower epithelium of the chamber, while spermatids develop in the upper epithelium. However, only 12% of Hartlaub's animals were hermaphroditic, the others were all female. Müller (1908) supplemented the former observations with more details. He found that the brood-chamber develops very early in development, even while the medusa is still attached. The fraction of hermaphroditic animals he found was higher, namely 35% of the fertile animals. Müller (1908) also reported that the spermatogonia can also be produced in small patches of the subumbrellar epidermis. Krumbach (1907) made many observations on the living animal and he describes its movements. He found that the velum tightly closes the umbrella. This he considered might reduce desiccation in case the animal is exposed to the air. Drzewina & Bohn (1913) studied the variability of the tentacle numbers in animals collected from nature. They found the following distribution among 39 animals: 1x8 tentacles, 1x7 tentacles, 30x6 tentacles, 7x5 tentacles. They also made regeneration experiments, observed anomalies, and investigated the influence of cyanide. The budding of medusae from the medusa bell includes also part of the radial canal, thus the medusa buds are of ento- and ectodermal origin (Hartlaub, 1886; Lengerich, 1923b). The development of the medusa bud includes also the formation of an entocodon. The development of the gametes takes place in the brood-chamber and the planulae are released by a rupture of the umbrella. The latter heals again after the release (Lengerich, 1923a). The histology of the medusa has been examined by several authors, e. g. Hartlaub (1886), Lengerich (1923a), Bouillon (1968), van de Vyver & Bouillon (1969), and Bouillon (1994: fig. 55). Bouillon (1968) also examined the histochemistry and ultrastructure of the adhesive organs. The haploid chromosome number is 6 (Makino, 1951; cited in Tardent, 1978). Hauenschild (1956) observed that the ability to produce gametes can irreversibly be lost in some clones, this either naturally or induced artificially. Hadrys *et al.* (1990) examined the feeding behaviour of the medusa. Ender (1997) analyzed the population structure using mitochondrial DNA sequences. Further experimental, developmental and structural details are given by Weill (1936), Hauenschild (1957a, b), Weiler-Stolt (1960), Schierwater (1989), Schierwater & Havenschild (1990), Schierwater *et al.* (1991, 1992), Kuhn *et al.* (1996), Schierwater & Hadrys (1998).

REMARKS: The synonymy is given by Bedot (1912, 1916, 1918), Mayer (1910), Lengerich (1923a), Kramp (1961), and Russell (1953). In its medusa phase, *Eleutheria dichotoma* is very characteristic and among the European medusae it can only be confounded with *E. claparedii*. The external medusae buds and the tentacles that are bifurcating in the middle make *E. dichotoma* immediately recognizable. In addition, *E. dichotoma* has usually five to six tentacles, while most *E. claparedii* have eight. Their polyps appear very similar and are perhaps not distinguishable.

Eleutheria claparedii Hartlaub, 1889

Figs 19D & 21

Eleutheria dichotoma – Claparède, 1863: 4, pl. 1 figs 4-10; Spagnolini, 1876: 312.[not *Eleutheria dichotoma* Quatrefages, 1842].*Eleutheria heteronema* Haeckel, 1879: 106.*Eleutheria diplonema* Haeckel, 1879: 106.*Eleutheria claparedii* Hartlaub, 1889: 665; Mayer, 1910: 95, fig. 49; Brinckmann-Voss, 1970: 80, figs 93-95.*Eleutheria claparedei* – Hartlaub, 1907: 129, fig. 128; Müller, 1911: 159, pl. 3 fig. 1; Drzewina & Bohn, 1913: 49, figs 26-37; Lengerich, 1922: 211, fig. 2; Lengerich, 1923a: 336, figs V-Z, A1-F1; Browne & Kramp, 1939: 274; Kramp, 1961: 59; Bouillon *et al.*, 2004: 88, fig. 48E-F.*Staurocladia claparedei* – Hartlaub, 1917: 401.

MATERIAL: Roscoff, France, September 2004, one medusa in plankton, mature male with medusae buds; one immature medusa with medusae buds on *Cystoseira* spec., developed eggs after 6 weeks of cultivation. 16S sequence of male medusa accession number AM088486.

DIAGNOSIS: *Eleutheria* medusa without brood-chamber, medusae buds within subumbrella, usually eight tentacles, tentacles bifurcated once in distal region and trunk thus clearly longer than branches, gonochoristic, nettle ring not conspicuous.

DESCRIPTION: Sedentary medusa clinging to seaweeds, flat, umbrella slightly shallower than a hemisphere, without jelly, usually eight to nine tentacles (range 5-10), not in phase with radial canals, tentacles relatively long when expanded, held horizontal, bifurcated at 1/4 to 1/6 from end, the two branches of equal length, upper branch ending in a capitulum, capitulum flat-button-shaped to oval, lower tentacle branch ends in adhesive pad, not much enlarged, used to cling to the substrate. One abaxial ocellus at base of each tentacle, colour red. Stomach large, filling nearly entire subumbrella, conical; four to six short radial canals; ring canal thick, underlying nettle ring inconspicuous but present. Velum conical, broad, usually closed and usually only opened for feeding, releasing medusae, gametes or excrements. Gonochoristic, gonads develop in stomach epidermis, without brood-chamber but embryos develop within subumbrella. Asexual multiplication by medusae budding frequent, buds arise from epidermis over radial canal in the subumbrellar cavity. Budding usually stops when gonads develop. Colours: Manubrium and medusae buds orange, rest whitish-cream or transparent. Nematocysts: stenoteles and desmonemes.

Polyp only known from cultivation experiments, colonies stolonal, swollen head, one whorl of 4-5 capitate tentacles, no filiform tentacles, further development unknown.

DIMENSIONS: Medusa bell diameter 0.4-0.5 mm, tentacle length up to 1 mm, tentacle capitula diameter 90-110 μ m. Claparède (1863) reported an egg size of 0.18-0.3 mm, spawned eggs observed in this study were 0.13 mm in diameter. Nematocysts of medusa: stenoteles, (11-27)x(8-19) μ m, ratio of length to width = 1.5; desmonemes (9-11.5)x(4.5-6) μ m, r=2.0. Polyp 0.7 mm high, tentacles 0.25 mm long (Drzewina & Bohn, 1913).

DISTRIBUTION: French Channel coast, Mediterranean (Naples). Type locality: Tahitou near St. Vaast la Hogue (Normandy, France).

BIOLOGY: The medusa was usually found clinging on macroalgae like *Ulva* spec. and *Fucus* spec. in the intertidal zone. In the English Channel, it is most frequent

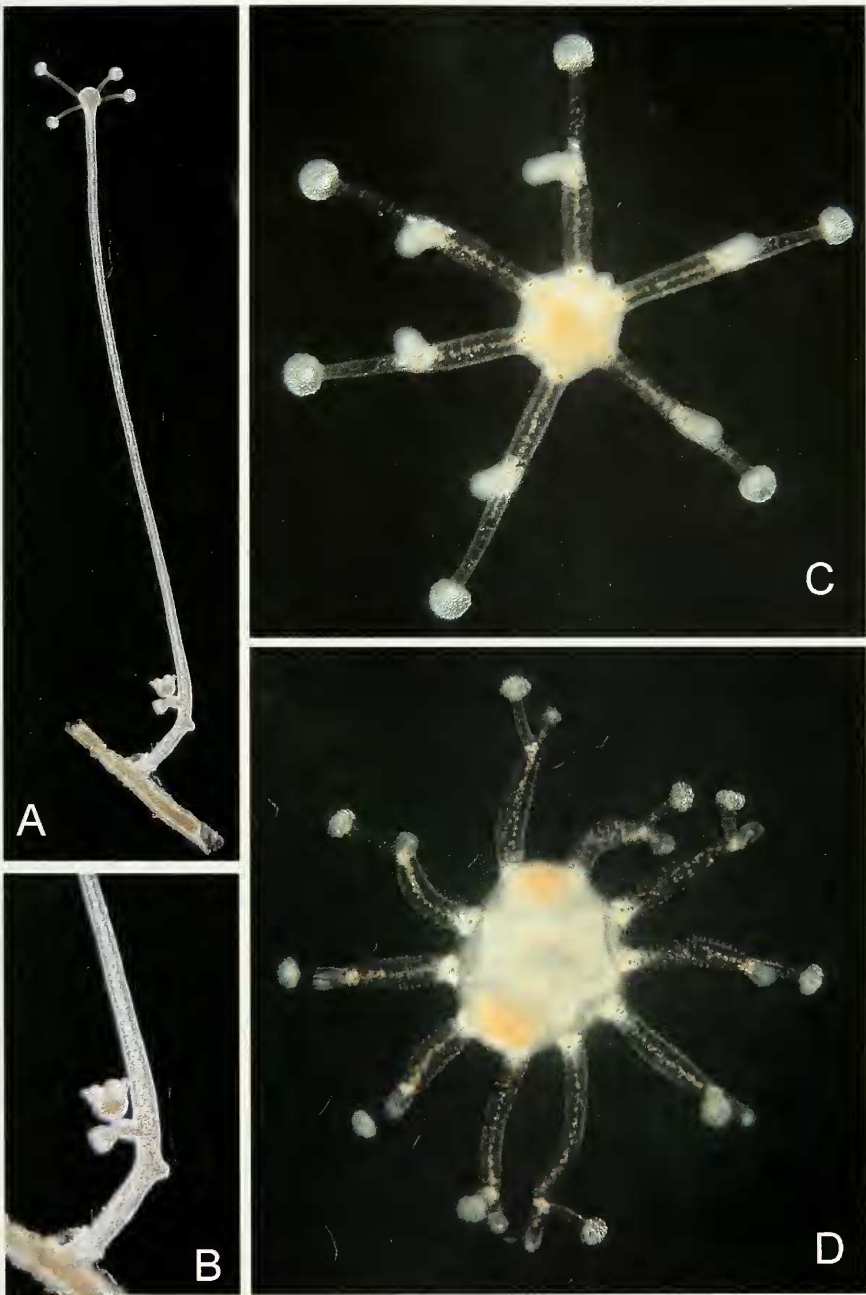


FIG. 19

A) *Eleutheria dichotoma* Quatrefages, 1842, cultivated polyp with medusa bud. B) as in A, enlarged medusa bud on gonostyle. C) *Eleutheria dichotoma*, mature medusa, an egg can be faintly seen. D) *Eleutheria claparedii* Hartlaub, 1889, medusa with two buds in the subumbrella.

in autumn and winter and disappears almost completely in spring (Teissier, 1965). Asexual production occurs all year round but especially during spring time, animals with mature gonads were observed from May to June and September to November.

ADDITIONAL DATA: The number of tentacles seems not strictly fixed genetically, as budded medusae may have other tentacle numbers than the mother medusa (Drzwina & Bohn, 1913).

Drzwina & Bohn (1913) examined more than 100 medusae and found that asexual medusae-budding stopped with commencing gonad maturation. One male animal observed for this study, however, had medusae buds and mature gonads. The female animal stopped budding before gonad development.

REMARKS: *Eleutheria claparedii* (original spelling) was named by Hartlaub (1889) by referring to a description of Claparède (1863) of an animal the latter had erroneously identified as *E. dichotoma*. Hartlaub (1889) states that he also found this species at Naples. He did not designate type material nor a type locality. As Hartlaub mainly referred to the description of Claparède (1863) based on material from Tahitou near St. Vaast la Hogue (Normandy, France), and as the major other descriptions of this species came from this population (Drzwina & Bohn, 1913; Müller, 1911), this locality is herewith selected as type locality. Hartlaub (1907) introduced the incorrect spelling *E. claparedei*, adopted by most subsequent authors. According to the ICZN [1999, 4th ed.; articles 31.1.1 and 31.1.3], the epithet can be formed in both versions, but as the spelling in the original publication was *Eleutheria claparedii*, this spelling must be used.

Before Hartlaub (1889), Haeckel (1879) had already introduced two new names for Claparède's animals: *Eleutheria heteronema* and *Eleutheria diplomema*. Although Haeckel's names are senior synonyms, they have never been used as valid names. Article 23.9.1.1 of the ICZN [1999, 4th ed.] is therefore invoked to declare them as invalid and *Eleutheria claparedii* Hartlaub, 1889 the valid name of this species.

Eleutheria claparedii was investigated in detail by Drzwina & Bohn (1913) and Lengerich (1923a).

The polyp has not yet been identified in the sea and only the young polyp without medusae buds is known from cultivation experiments. Drzwina & Bohn (1913) found them indistinguishable from young polyps of *E. dichotoma*.

Genus *Staurocladia* Hartlaub, 1917

TYPE SPECIES: *Eleutheria vallentini* Browne, 1902, by designation of Hartlaub (1917).

SYNONYMS: *Wandelia* Bedot, 1908; *Cnidonema* Gilchrist, 1919.

REFERENCES: Hartlaub (1917); Gilchrist (1919); Browne & Kramp (1939); Kramp (1961); Bouillon (1985); Petersen (1990); Bouillon & Boero (2000).

DIAGNOSIS: Hydroid stolonal or sessile, hydranths with an oral whorl of capitate tentacles, with or without aboral filiform tentacles; medusa buds borne singly on hydranth body immediately above filiform tentacles or in similar position when these are absent. Medusa adapted to a crawling and walking mode of life, exceptionally still able to swim; without brood-chamber above manubrium; with or without continuous or interrupted nematocyst ring along margin; gonads around manubrium or developed on

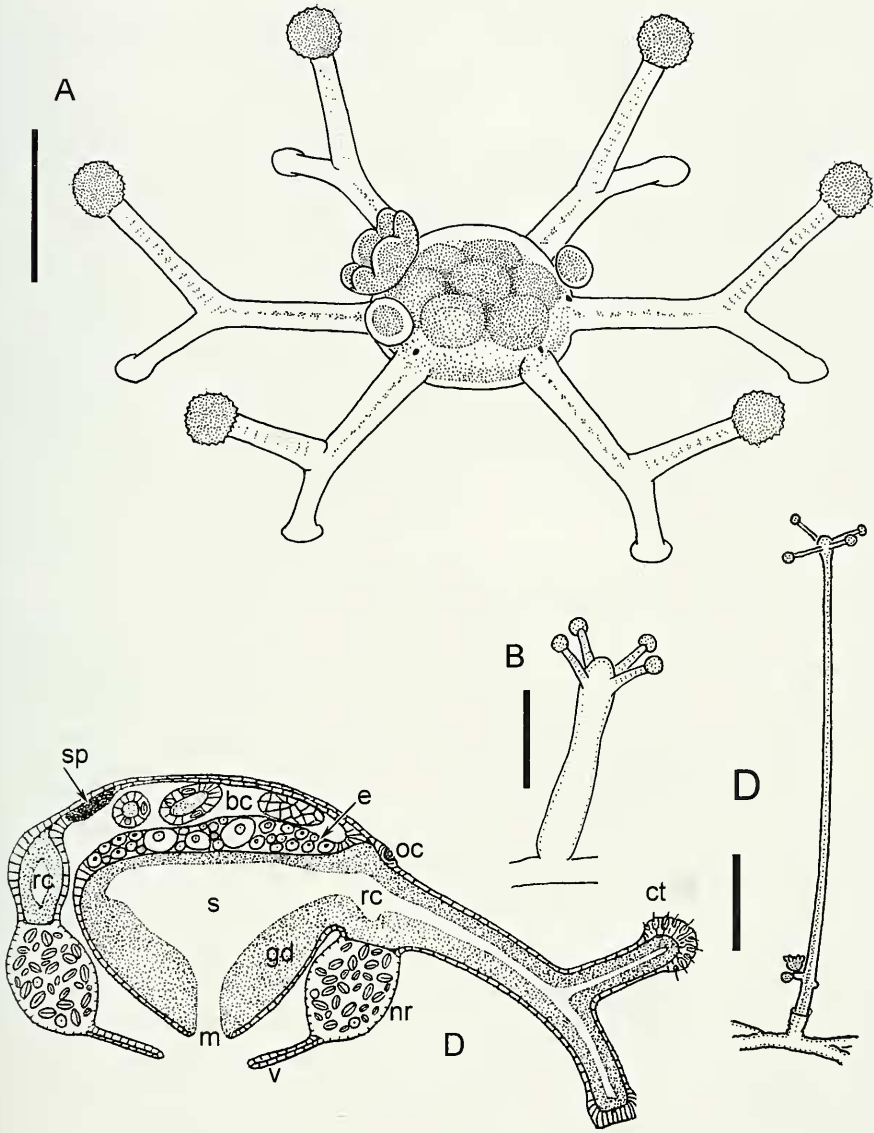


FIG. 20

Eleutheria dichotoma Quatrefages, 1842. A) Medusa with developing embryos in brood-chamber, after living material, scale bar 0.5 mm. B) Polyp stage obtained from medusa shown in figure A, scale bar 0.5 mm. C) Polyp with medusae buds, modified after Hauenschild (1956). D) Schematic organization of the medusa in a vertical section, right half perradial, left half interradial; modified after Lengerich (1922). Abbreviations: bc brood-chamber with developing embryos, ct upper branch of tentacle with nematocyst knob (capitulum), e developing eggs, gd gastrodermis, m mouth, nr nettle-ring, oc ocellus, rc radial canal, s stomach, sf lower branch of tentacle with adhesive organ, sp male gonad, v velum.

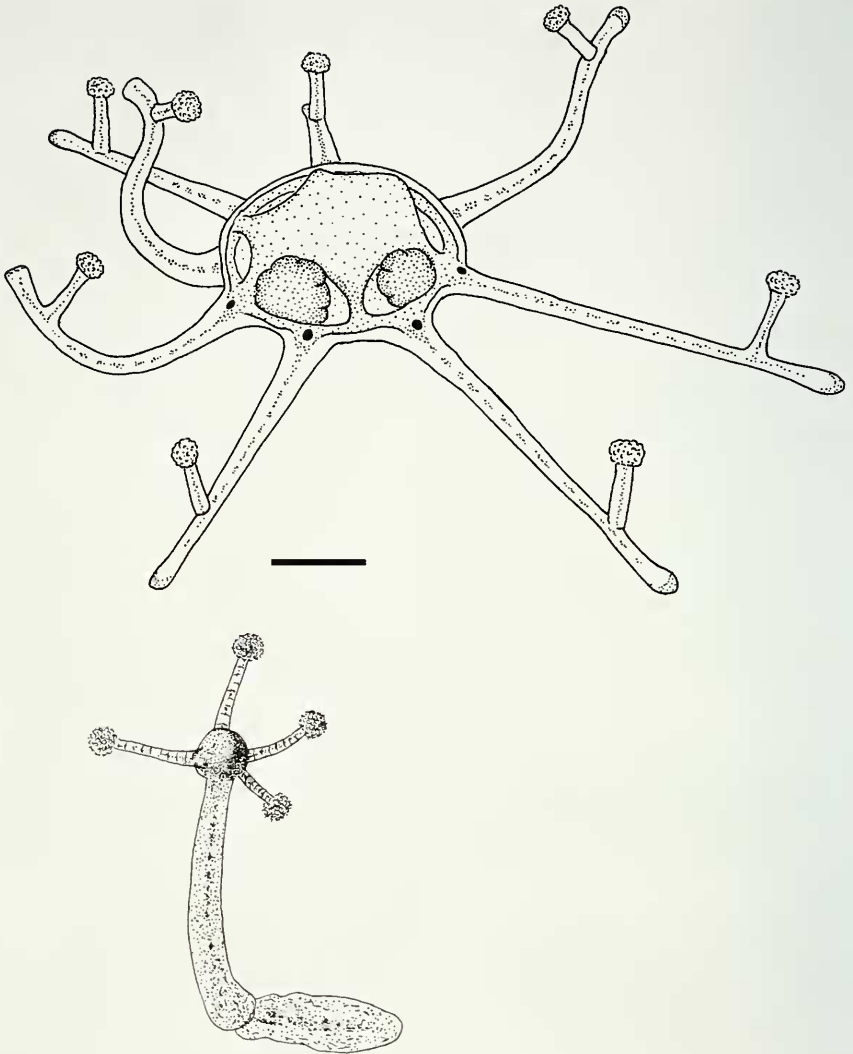


FIG. 21

Eleutheria clapedii Hartlaub, 1889. A) after living animal from Roscoff, note the two medusa buds within the subumbrella (stippled darker), scale bar 0.2 mm. B) Young hydranth, after Drzewina & Bohn (1913).

manubrial protrusions; with six to eleven radial canals, some bifurcating shortly distal to manubrium; mouth circular with or without nematocyst knobs; with up to 60 marginal tentacles, dichotomous, upper branch with several nematocyst clusters, lower with adhesive organ; often asexual reproduction by medusa budding or by fission; with abaxial ocelli at tentacle base.

REMARKS: The problems concerning the distinction of *Eleutheria* and *Staurocladia* have been discussed above under "Remarks" at the family level. There is only one species in the European fauna.

Staurocladia portmanni Brinckmann, 1964

Fig. 22

Staurocladia portmanni Brinckmann, 1964: 693, figs 1-10; Brinckmann-Voss, 1970: 82, figs 96-98, pl. 6 figs 1-3; Bouillon *et al.*, 2004: 90, fig. 481-J.

MATERIAL EXAMINED: *Staurocladia portmanni*, syntypes BMNH 1963.12.10.2, Ischia, Naples, 2 mature medusae. – *Staurocladia portmanni* syntype BMNH 1963.12.10.1, Italy, Gulf of Sorrento, Vico Equense, polyp colony.

DIAGNOSIS: Hydroid with one oral whorl of capitate tentacles and an aboral whorl of six filiform tentacles, short perisarc covered pedicel, medusae budded directly from hydranth body above filiform tentacles. Medusa clinging and creeping on substratum, but also able to swim freely, five to ten branched radial canals, each sending a protuberance into mesogloea, 18-24 tentacles, bifid, nematocyst clusters terminal and on oral and aboral sides of upper branch, plus an additional lateral pair near branching point; five interradial manubrial pouches; gonad surrounds entire manubrium; mouth with five nematocyst clusters.

DESCRIPTION (after Brinckmann, 1964; Brinckmann-Voss, 1970; Bouillon, 1966; and own observations): Hydroid forming small, stolonal colonies. Stolons ensheathed by perisarc which extends up to the short pedicel; hydranth with three to five capitate tentacles in an oral whorl and six filiform tentacles at base of hydranth body, number of filiform tentacles constant; usually one, rarely two medusae buds above filiform tentacles. Preoral cavity present. Nematocysts: stenoteles. Colour: pink-orange. Medusa-bud development very slow, taking up to 50 days.

Newly liberated medusa 0.6-0.7 mm in diameter; seven to nine tentacles, bifid, oral branch with terminal adhesive end, upper branch short and with one terminal nematocyst cluster, sometimes also an additional aboral one, two lateral nematocyst clusters on common trunk near bifurcation always present; five to ten radial canals, number not increasing with further development, protuberances small.

Adult medusa with bell-shaped umbrella, wider than high. Manubrium not extending beyond velum, with five protruding stomach-pouches in middle, mouth with five spherical nematocyst clusters. Gonads surround manubrium and stomach pouches without perradial interruptions, gonads get separated into five sections only where radial canals are adnate to top of the manubrium; gonochoristic, no medusa budding. Five radial canals originating near centre of top of manubrium, then sandwiched between subumbrella and broad base of manubrium for a third of their length, some branching dichotomously so that up to ten radial canals reach the circular canal, at upper third of each radial canal an upright, finger-like protuberance that penetrates into mesogloea; radial canals widen bulb-like before joining circular canal. Tentacles 16-25 in number, hollow, lumen communicates with circular canal; each tentacle bifurcated at about the middle; lower branch with terminal adhesive pad; upper branch with terminal nematocyst cluster (capitulum), plus two to five aboral, and two to four aboral nematocyst clusters; common trunk bears additionally two lateral nematocyst clusters near branching point. Each tentacle contains one basal, abaxial ocellus. Border

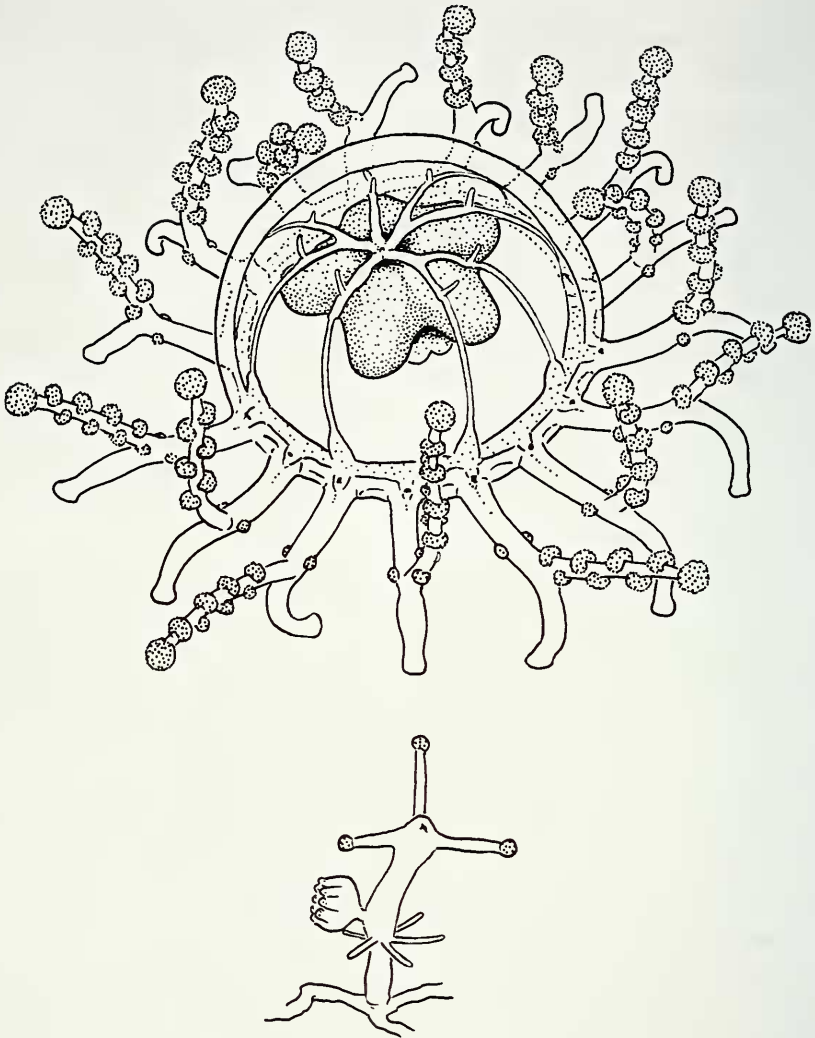


FIG. 22

Staurocladia portmanni Brinckmann, 1964, modified after Brinckmann-Voss (1964), above: mature medusa, below: polyp with medusa bud. For size see text.

between exumbrella and velum is thickened with nematocysts. Colours: gastrodermis of stomach, circular canal, and tentacles red-orange; upper part of radial canals and protuberances contain a white pigment, same pigment is also found in the distal part of radial canals where they widen and join circular canal. Nematocysts: stenoteles, desmonemes, and a large, unidentified capsule.

DIMENSIONS: Hydranth body 1.5-2 mm in height, Adult medusa 4-6 mm in diameter, bell-height 2.5-5 mm.

DISTRIBUTION: Only known from the region of Naples (Tyrrhenian Sea, Mediterranean). The material used for the original description came from the Gulf of Sorrento (polyp stage) and the island of Ischia (medusa). Under type locality, Brinckmann (1964) gives only the registration number BMNH 1963.12.10.1. According to the label of this specimen in the BMNH, it came from Vico Equense in the Gulf of Sorrento and this locality must therefore be assumed to be the type locality.

BIOLOGY: The medusae of *S. portmanni* are found in *Posidonia oceanica* beds in depths of 15-35 m from end of May to begin of July. The hydroid was found on algae like *Udothea* sp. and *Halimeda tuna* in a depth of 30 m. The medusa development is extraordinarily slow, it takes up to 50 days from the first bud to the liberation and another 40-60 to sexual maturity.

The medusa of *S. portmanni* is able to creep as well as to swim freely. More details on its behaviour are given in Brinckmann-Voss (1970).

Genus *Dendronema* Haeckel, 1879

TYPE SPECIES: *Dendronema stylodendron* Haeckel, 1879 by monotypy.

REFERENCES: Haeckel (1879); Kramp (1961); Bouillon & Boero (2000).

DIAGNOSIS: Cladonematidae with branched oral tentacles; umbrella bell-shaped, with an apical cavity above manubrium.

REMARKS: A problematic genus containing a single, doubtful species, see discussion below.

Dendronema stylodendron Haeckel, 1879

Fig. 23

Dendronema stylodendron Haeckel, 1879: 110, pl. 7 fig. 8; Lengerich, 1922: 210; Kramp, 1955: 307; Kramp, 1959: 96; Kramp, 1961: 58.

MATERIAL: None examined, likely no type material exists.

DIAGNOSIS: As for genus.

DESCRIPTION (after Haeckel, 1879): Umbrella bell shaped, height 9 mm, diameter 6 mm; with pointed, conical apical process, nearly twice as high as broad. Manubrium spindle-shaped, continued into mesogloea as apical cavity, in proximal half with four egg-shaped gonads, mouth with four dichotomously branched oral tentacles (50-60 ends) reaching down to velum level. Four radial canals that divide close to manubrium into two branches. Eight tentacles, each with an ocellus that has a lens, each tentacle divided into two principal branches, of which the adaxial one branches two times and bears four adhesive ends, the abaxial branch divides dichotomously several times and bears many nematocyst knobs. Colours: manubrium and apical cavity reddish-yellow; tentacles, radial- and circular canals red; ocelli black.

DISTRIBUTION: Known from original description only, type locality: Lanzarote, Canary Islands.

REMARKS: Besides its first description, *Dendronema stylodendron* has never been reported again and some authors doubted its existence, e. g. Lengerich (1923a) lists it as a synonym of *Cladonema radiatum*. Kramp (1955, 1961) thought that this is

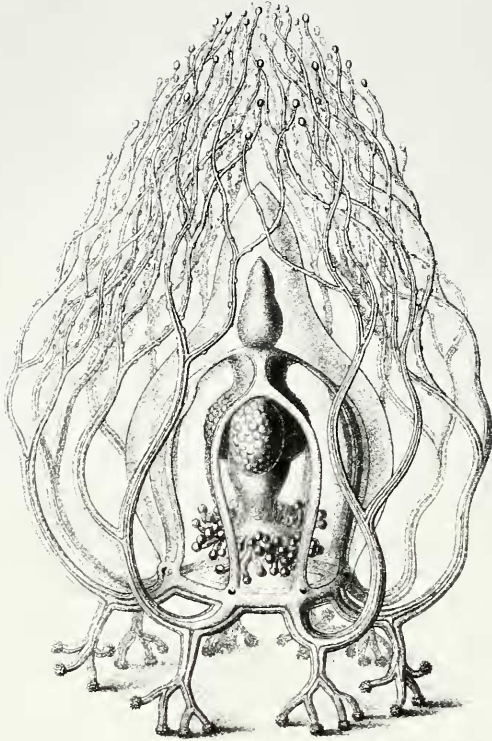


FIG. 23

Dendronema stylodendron, after Haeckel 1879.

unlikely, but nevertheless classified it as doubtful (Kramp, 1959). Haeckel based his description of on a living specimen he collected at Lanzarote. The animal is remarkably large for this family and his drawings are quite detailed. So, it seems quite unlikely that Haeckel confounded it with the much smaller *Cladonema radiatum*. However, the species remains somewhat doubtful until it can be found again.

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INDEX

- | | |
|--|---|
| <i>Acanthella</i> , 341 | <i>cocksii</i> , <i>Candelabrum</i> , 341 |
| Acaulidae, 326 | <i>corynaria</i> , <i>Hydra</i> , 370 |
| <i>Acaulis</i> , 328 | Corynidae, 380 |
| <i>Acaulooides</i> , 330 | <i>Dendronema</i> , 391 |
| <i>Allmani</i> , <i>Cladonema</i> , 376 | Dendronemidae, 371 |
| <i>ammisatum</i> , <i>Acaulooides</i> , 330 | <i>dichobdella</i> , <i>Eleutheria</i> , 381 |
| <i>anisonema</i> , <i>Eleutheria</i> , 381 | <i>dichocnida</i> , <i>Eleutheria</i> , 381 |
| <i>Arum</i> , 341 | <i>dichotoma</i> , <i>Eleutheria</i> , 381 |
| <i>Blastothela</i> , 328 | <i>diplonema</i> , <i>Eleutheria</i> , 384 |
| <i>Boreohydra</i> , 334 | <i>disticha</i> , <i>Pennaria</i> , 364 |
| Boreohydridae, 334 | <i>Dujardinii</i> , <i>Cladonema</i> , 376 |
| <i>californicum</i> , <i>Cladonema</i> , 379 | <i>Eleutheria</i> , 380 |
| Candelabridae, 340 | Eleutheriidae, 371 |
| <i>Candelabrum</i> , 341 | <i>Eucoryne</i> , 364 |
| <i>Cladocoryne</i> , 368 | <i>floccosa</i> , <i>Cladocoryne</i> , 368 |
| Cladocorynidae, 368 | <i>fritchmanii</i> , <i>Candelabrum</i> , 346 |
| <i>Cladocorynopsis</i> , 368 | <i>Gegenbauri</i> , <i>Cladonema</i> , 376 |
| <i>Cladonema</i> , 375 | <i>gemmaipara</i> , <i>Eleutheria</i> , 381 |
| <i>cladonema</i> , <i>Stauridium</i> , 376 | <i>gigantea</i> , <i>Monocoryne</i> , 381 |
| Cladonematidae, 371 | <i>Globiceps</i> , 364 |
| <i>claparedei</i> , <i>Eleutheria</i> , 384 | <i>haeckelii</i> , <i>Margelopsis</i> , 356 |
| <i>claparedii</i> , <i>Eleutheria</i> , 384 | <i>Halocordyle</i> , 364 |
| <i>Clavatella</i> , 380 | <i>Halocordyle disticha</i> , 364, 367 |
| <i>Climacocodon</i> , 356 | Halocordylidae, 363 |
| <i>cnidobdella</i> , <i>Eleutheria</i> , 381 | <i>hartlaubii</i> , <i>Margelopsis</i> , 361 |
| <i>Cnidonema</i> , 373 | <i>helleri</i> , <i>Polycoryne</i> , 370 |

- heptanema*, *Eleutheria*, 381
Herpusa, 380
heteroclada, *Eleutheria*, 381
heteronema, *Eleutheria*, 384
hexanema, *Eleutheria*, 381
Hydra corynaria, 370
ilonae, *Acaulooides*, 332
krohni, *Eleutheria*, 381
Krohni, *Cladonema*, 376
leuckarti, *Protohydra*, 338
Lobocoryne, 368
 Margelopsidae, 356
Margelopsis, 356
mayeri, *Cladonema*, 376
minor, *Monocoryne*, 353
Monocoryne, 351
myersi, *Cladonema*, 380
Myriocnida, 328
Myriothela, 340
 Myriothelidae, 340
nanna, *Psammohydra*, 336
nematophora, *Similomerona*, 325
novae-zelandiae, *Cladonema*, 376
novaezelandiae, *Cladonema*, 380
octonema, *Eleutheria*, 381
pacificum, *Cladonema*, 380
pelagica, *Cladocoryne*, 370
Pelagohydra, 356
Pelagohydridae, 356
Pennaria, 364
 Pennariidae, 363
pentanema, *Eleutheria*, 381
perkinsii, *Cladonema*, 376
phrygium, *Candelabrum*, 346
Polycoryne, 368
portmanni, *Staurocladia*, 389
primarius, *Acaulis*, 328
prolifera, *Clavatella*, 381
Protohydra, 338
 Protohydridae, 337
Psammocoryne, 330
Psammohydra, 336
purpurea, *Spadix*, 341
radiatum, *Cladonema*, 375
sargassensis, *Cladocoryne*, 370
serpentarii, *Candelabrum*, 341
Similomerona, 325
simplex, *Boreohydra*, 334
simplex, *Cladocoryne*, 370
singularis, *Tricyclusa*, 353
Spadix, 341
Stauridia, 375
stauridia, *Coryne*, 376
Stauridium, 375
stauridium, *Syncoryne*, 376
 Stauriidae, 371
Staurocladia, 372, 386
stylo dendron, *Dendronema*, 391
stylostoma, *Margelopsis*, 353
Symplectanea, 351
 Symplectaneidae, 340
tetranema, *Eleutheria*, 381
Tiarella, 353
Tricyclusa, 353
 Tricyclusidae, 353
uchidai, *Cladonema*, 380
ulvae, *Herpusa*, 381
vallentini, *Eleutheria*, 386
verrucosum, *Candelabrum*, 349
Wandelia, 386